

Native afforestation: Review of Germination

Te Uru Rākau – New Zealand Forest Service Technical Paper No: 2024/03

Prepared for Te Uru Rākau
by Mānuka Farming NZ
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ISBN No: 978-1-991285-59-1 (online)

June 2024

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“Because seeds are so central to people’s cultures and food systems, to control seeds is to control life.”

Michael Fakhri, UN Human Rights Council Special Rapporteur -
Seeds, Rights to Life and Farmers Rights

Executive Summary

This literature review was commissioned by Te Uru Rakau - New Zealand Forest Service (TUR) to assess the current state of knowledge and research of germination of tall native New Zealand tree species. It summarises published literature, identifies knowledge gaps and suggests areas of focus for further research with recommendations for improving germination traits of native tree seeds. Topics covered include: seed production, seed dormancy, hormonal impacts on the germination process, mycorrhizal associations and impacts on germination, abiotic factor influence, amendments to improve controlled germination, and use of transplanters and other potential technological improvements for nursery production of native tree seedlings. This review summarises published data, identifies knowledge gaps in such literature, suggests areas of focus for further research and provides recommendations to improve germination of native trees in the future.

Key takeaways

Pollen limitation constrains plant reproductive success, leading to reduced seed quantity and quality, increased self-pollination, and potential inbreeding depression. New Zealand woody species face pollen limitation due to factors like fragmented populations and self-incompatibility, impacting the seed supply chain and seedling recruitment. Declining populations of pollination providers like birds and insects is a significant threat to seed production in many species.

Self-compatible tree species like kōwhai and kōtukutuku suffer up to 80% inbreeding depression, impacting seed fitness. Nurseries face challenges collecting seeds from small populations, risking seedling survival.

Creating favourable conditions for maternal plants may provide an opportunity for improved germination outcomes through increased resource allocation during seed production and reduced dormancy characteristics. Disparities in germination percentages between populations have been observed in New Zealand native species like hutu, pūriri, tarata, karo, and southern beech, emphasising the need to keep records of seed collection locations and germination outcomes.

Seed dispersal plays a crucial role in the success of plant germination, influencing factors such as dormancy, allelopathic effects, and microsite influence. In New Zealand, unique flora features a higher proportion of fleshy-fruited species, with approximately 70% relying on animal dispersers. Tree management strategies should consider the roles of both native and introduced species in seed dispersal when considering how to increase germination in natural ecosystems.

Alleviating seed dormancy is crucial for successful germination and can involve pre-germination treatments such as stratification using different temperature regimes, mechanical scarification, and specific storage conditions. Many New Zealand tree dormancy types are suggested, but not confirmed. There is opportunity to explore germination amendments and protocol improvements focused on this area.

Climate change may impact native forest distribution, increase fire risks, and alter masting schedules. Elevated CO₂ levels are likely to affect nutrient cycling and plant growth, potentially intensifying competition among species. The increasing weather variability and temperatures is likely to benefit invasive plants, affecting native seed banks and increasing germination competition. Increased competition for pollination services, influenced by non-native flora, could also reduce the reproductive capacity of native species.

Successful germination microsites are multidimensional and transient, influenced by sunlight, moisture, precipitation, wind, and temperature. Woody debris creates valuable microsites. Climate risks such as floods, fires, drought, slip and wind erosion create variable effects, pushing germination and recruitment towards early successional species. Soil nitrogen and phosphorus levels influence the eventual species assemblage of trees, driving seed rain and seed bank composition. Higher acidic conditions, often due to human activities, impact nutrient availability in soil and can hinder germination. Generally, light availability positively influences germination, as seen in canopy gaps driving species richness. Shady microsites with higher moisture favour native species germination in many circumstances, although shade tolerance varies among species.

Mycorrhizal fungi, crucial for nutrient absorption and ecosystem functioning, have complex roles in germination. Hormones like strigolactones, essential in creating fungal symbiosis, may overlap with seed germination signals. Bacteria, notably methylotrophic types, have been observed in other locations internationally to

impact germination. Likewise, endophytic actinobacteria have been observed to enhance growth. The impact of bacteria on native tree germination needs further exploration.

Approximately 220 plant pathogens, such as myrtle rust, have invaded New Zealand. Controlling disease spread in nurseries is crucial for successful seedling production especially for nurseries who also produce exotic species. Native myrtle species, some being highly susceptible to myrtle rust, face serious impact, potentially leading to local extinction due to recurring infections of reproductive tissues. Resistance to myrtle rust is variable between species. Nurseries in New Zealand face logistic risks from both potential lack of seed availability due to myrtle rust infection of wild populations and dangers of rust disease spread in nursery production.

Exotic woody species in New Zealand influence native plant succession, with shade tolerance of native seeds crucial for successful replacement. Gorse and invasive brooms often facilitate native regeneration, while radiata pine and blackberry create varying conditions, often dependent on moisture availability. The Department of Conservation (DOC) has created decision-making tools to assist in predicting native success under non-native canopies to inform weed management.

Exotic fauna such as deer, pigs, possums, mice and rats can cause significant adverse impacts on native plants via feeding habits, soil disturbance, faecal impact on mycorrhizal populations, and other mechanisms. Pest control is therefore an essential part of management when considering long term native tree germination impacts.

The mycorrhizal associations of mānuka and kānuka assist with later successional tree species colonisation. Tutu, being a nitrogen fixer, enhances soil conditions for seed germination, though its toxicity may limit applications. Tree ferns provide a potential sheltered germination pathway for shade-loving native tree species, though native podocarps may be negatively affected. Bryophytes (mosses, liverworts) exhibit some allelopathic impacts with seed germination and early root development, emphasising need for management in nursery germination activities.

Animal ingestion can affect germination outcomes through fertilisation, scarification, and deinhibition effects. Bird species appear to be the most relevant native animal group.

Direct seeding is an alternative to transplanting seedlings, offering cost and timeline efficiencies, but success hinges on various factors. Challenges include seed availability, uncertain sowing times, variable germination timelines, and managing vegetation competition. Research indicates that outcomes are influenced by factors like soil disturbance, grazing, and herbicide usage with early successional species like kāpuka and mānuka being best suited.

Seed Enhancement Technology (SET) focuses on methods to boost seed and seedling performance. Techniques like halopriming, osmopriming, biopriming, hormonal priming, and nanotechnology application can improve germination and seedling vigour. Seed coating may also provide opportunities to improve germination outcomes and seed handling in the nursery. However, research in this area is almost exclusively conducted on agricultural species.

The integration of Te Ao Māori and scientific literature offers valuable insights, particularly in research approaches and applications. Building relationships with Māori communities enhances meaningful engagement for conservation and restoration efforts. Species and seed conservation in New Zealand involves collaboration with Māori, notably through the Māori Biosecurity Network Te Tira Whakamātaki, contributing to seed banking, indigenous seed conservation protocols, and potential around long-term management needs for seed producing tree populations.

Transplanting ("pricking out"), requires more in-depth research and development if it is to be successfully deployed at scale in commercial nurseries working with native plants. Technology exists to both increase and improve outputs, but adoption by native tree production nurseries will be challenging.

Seed storage protocols are critical and need to be adapted for specific native species. Recalcitrance (sensitivity of seed to desiccation) in some native tree species prevents conventional seed banking options with no current solution outside of maintaining living collections. To support native afforestation in New Zealand, efficient germination protocols are crucial for nurseries. Appendix 1 contains a full set of protocols and germination recommendations.

Knowledge of the factors affecting germination of New Zealand's native tall tree species has expanded beyond controlled protocols. Much information can be gleaned to improve natural regeneration, highlight potential threats, and improve seed collection quality. Further, there can be inspiration taken from agricultural studies to

improve germination outcomes. Germination is an essential part of creating sustainable tree populations as New Zealand moves to improve conservation outcomes and environmental stewardship into the future.

Introduction

The germination of native tree seeds in Aotearoa New Zealand plays a pivotal role in the conservation and restoration of the country's unique and ecologically diverse forests. With a rich collection of indigenous tree species, New Zealand boasts flora that are both ancient and highly adapted to their environments, with 86% of species being endemic (de Lange & Rolfe 2010). Our trees fall within four categories: tree ferns, conifers, hardwoods, and monocotyledons, with the forests having the distinctive feature of being overwhelmingly evergreen when compared to other temperate regions of the world (Wardle & Platt 2011). Native trees face numerous challenges, including ecological degradation, climate change, and invasive species which threaten their reproductive capabilities and ultimately their survival. Over the past several years, there is increasing interest in native afforestation and thus in further development of the native forestry industry as part of the primary sector and as an essential part of addressing land use concerns across New Zealand. Examples of this include the creation of mānuka plantations for the production of mānuka honey, new regulations around waterway protection, deployment of the One Billion Trees Programme, changes to the emissions trading scheme (ETS), and the re-establishment of Te Uru Rākau - New Zealand Forest Service in 2018. There is also increasing interest from the public around environmental restoration and growing recognition of the important functions and roles provided by native forests as we seek to mitigate the impact of climate change. Understanding the intricacies of seed germination in this context is essential for developing effective nursery practices, conservation strategies, and reforestation efforts; germination is quite literally the starting point for native afforestation.

This literature review of native tree germination builds upon three previous germination reviews as published in 1991 (Fountain & Outred), 1994 (Bannister & Jameson), and 2007 (Rowarth et al.), focusing on information and analyses created in the past 15 years. Keyword searches were used, including terms such as "New Zealand native tree germination," "seed germination," "seed production," and specific species names, were employed to retrieve pertinent scholarly literature. Alongside journal articles, literature from industry sources and published books were also utilised. Relevance to and focus on New Zealand native tall trees was emphasised, though international sources or global analyses are discussed where New Zealand specific information was not available. Literature was excluded if it contained no pertinence to germination or tree seed production. This review will provide an updated set of practical protocols (see Appendix 1) around native tree germination and will explore factors influencing this critical stage of a tree's life cycle. These factors include the reproductive strategies of key species, biotic and abiotic influences, and new technological options for improved germination. As part of the exploration of expanding nursery technology, search terms included, "seed enhancement technology," "seedling transplanting," and "seedling nursery automation". The focus of this review is tree species, but smaller woody species are also discussed where relevant to specific tall woody species.

What is Germination?

Seed germination is the physical and metabolic transformation from seed to seedling, changing from a quiescent state to actively growing. The advancement of germination is regulated by hormonal interactions (endogenous) and environmental (exogenous) factors, with seed dormancy, or lack thereof, responding to both aspects. Seed germination at its most basic necessitates moisture, oxygen, and warmth, the optimal temperature range falling between 10 to 42°C (Broome 2012). During germination, seeds undergo rehydration via imbibition which puts into motion the series of metabolic events that comprise germination. Seed imbibition (Phase 1) is the process whereby water enters the dry cell walls composed of cellulose, proteins, and reserve polymers. Dry seeds quickly take up water, though not equally throughout the seed mass, as certain physical structures can inhibit water absorption (Bewley & Black 1994). Hydration allows the biogenesis (typical of oil-storing seeds) or repair and reactivation (typical of starch-storing seeds) of mitochondria and resumption of the pathways of energy metabolism, which are primarily glycolysis and the pentose phosphate pathway (Nonogaki et al. 2010). This transition into Phase 2 is also a period of significant genetic repair and transcription, leading to the synthesis of hormones, with gibberellin (GA) and abscisic acid (ABA) being the main regulators of germination events (Yamaguchi et al. 2007). As the seed components absorb water, they undergo softening and expansion, typically doubling the initial seed size (Broome 2012). This places considerable pressure on the seed coat, facilitating the emergence of the embryonic root

and shoot (radicle and plumule) structures, which is the end of germination in the strict definition (end of Phase 2, Nonogaki et al. 2010). The split in the seed coat accelerates water and oxygen absorption by the embryo and mobilises energy reserves, increasing the rate of cellular division, transforming the radicle to root for absorption of water from soil, and of the plumule to shoot for photosynthesis (Phase 3).

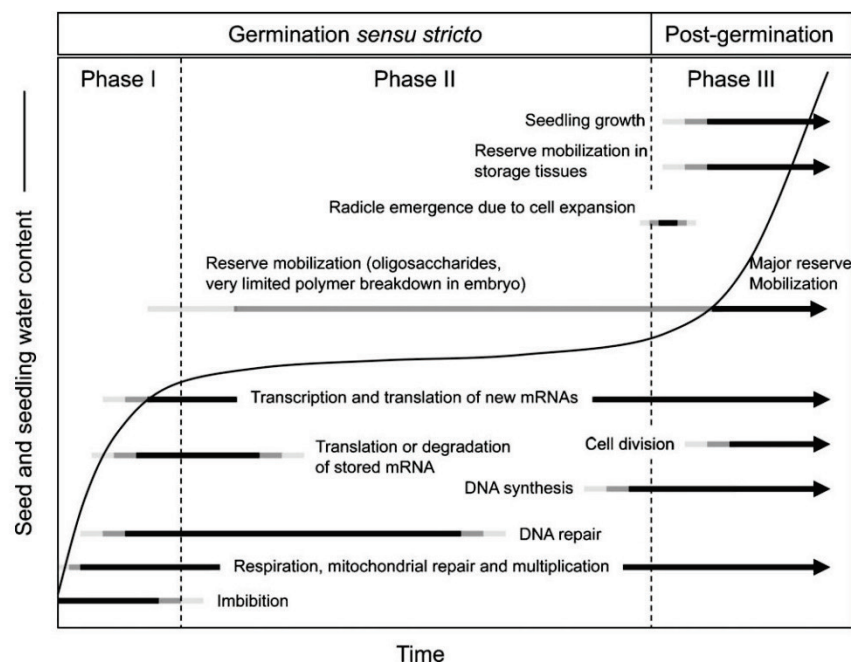


Figure 1: Events occurring during germination (Phase 1 and 2) and early seedling growth (Phase 3). Curved line demonstrates water intake across phases. The timing of events varies by species and is influenced by environmental conditions. From Nonogaki et al. 2010.

During germination, hormonally activated enzymes break down the seed's energy reserve into simpler molecules which are then transported to emerging seedling structures for their development. This encompasses Phase 3 of the less strict definition of germination (Millerd & Thomson 1975, Nonogaki et al. 2010). When this energy reaches the growing tissues, the embryo's root extends into the soil, serving as an anchor for the emerging shoot, while also absorbing minerals and water from the soil solution. Thus, full germination concludes when the shoot breaks through the soil surface. Throughout this growth stage, the plant relies entirely on the nutritional resources stored within the seed, primarily located within the cotyledons and endosperm (Millerd & Thomson 1975, Broome 2012, Joshi 2018).

This operative definition of germination ending at the plumule breaking the soil surface has determined which influences are specifically discussed further herein. Namely: seed development and production, seed dispersal and microsite interactions, the impacts of soil condition and the local species community. Beyond this, known improvements to specific species protocols as well as nursery and seed enhancement technologies that might be applied to New Zealand tree species are explored as options for implementing interactions into the seedling production supply chain.

1. Seed Quality and Dispersal

When considering germination, especially in a controlled setting like a nursery, quality and quantity of seed will determine the final output of the production system. Certain aspects of tree reproductive strategies and interactions with population size and genetics will impact the seed production capacity and viability. This section aims to highlight issues faced by trees during reproduction and discuss potential points of risk or opportunity for those who manage seed supplying populations.

1.1 Pollen Limitation

Pollen limitation occurs when a plant's reproductive success is constrained by the availability of pollen, a reduced transfer of pollen to stigma, or by lowered quantity and quality of pollen donors. Pollen limitation can have several adverse effects on seed production: plants may produce fewer seeds or lower-quality seeds, as fewer ovules are fully fertilised from a suitable pollen source; it can also lead to increased self-pollination (selfing), which reduces genetic diversity within a population (Robertson et al. 2011, Etten et al. 2015, Baskin & Baskin 2018). Reduced genetic diversity can lead to inbreeding depression within a population, reducing not only the fitness of seeds, but of seedlings. In general, pollen performance can be affected by various environmental factors during pollen development, including herbivory, temperature and soil nutrients and pH (Lankinen 2000), though paternal effects (i.e. related to pollen) on seed and seedling vigour are considered smaller than maternal effects.

Despite there being a number of potential negatives, experimentation exploring pollen limitation has not produced widespread consensus on the specific root causes of negative outcomes (Baskin & Baskin 2018). There is some evidence globally (14 of 30 case studies 46.7%, 15 plant families) that a low pollen load versus a high pollen load reduces germination percentage and/or rate (Baskin & Baskin 2015, van der Walt 2018). In New Zealand woody species, there is evidence that pollen limitation does reduce seed production in particular, so it is an area that needs consideration in the wider context of the seed supply chain and seedling recruitment with specifics discussed in the 'inbreeding depression' section below (Robertson et al. 2011, Etten et al. 2015). Pollen limitation can happen due to various reasons, but most relevant to the woody species of New Zealand are: lack of pollination services, fragmented population dynamics, self-incompatibility (i.e. inability to self pollinate), and a relatively high amount of species with separately sexed individuals (dioecious species).

1.2 Pollinators in New Zealand

It has been shown that in bird-pollinated species, pollen limitation is rated as moderate to severe, with 73% of the tested species within the top 30% of the limitation effect (Anderson et al. 2011, Kelly et al. 2010). This issue is due to pollinator breakdown and impacts both self-compatible and self-incompatible plant species, though Robertson et al. (2008) showed that 16 self-incompatible shrubs had a higher chance of encountering the effects of pollen limitation. Currently, the most important pollinator birds are tui, silvereyes (tauhou), and bellbirds (korimako), which together accounted for 89% of flower visits; with exotic birds fulfilling 5% of visits (Kelly et al. 2006). In bird sanctuary locations, stitchbirds (hihi) contributed 15.4% of visits, which alongside kaka and kokako are thought to have been important pollinators in New Zealand prior to human habitation due to their brush-tongue (Thorogood 2007, Kelly et al. 2010). The changes in bird pollinator populations are due to a number of extinctions as well as significant declines in bird populations since the arrival of humans and other invasive mammalian species (Kelly et al. 2010).

Insects were previously thought to be sufficient as replacement to bird pollination (Godley 1979, Clout & Hay 1989, Anderson et al. 2016), but this has now been dismissed due to several bird exclusion/insect inclusion experiments (Newstrom & Robertson 2005). New Zealand has 32 native bee species, who are all solitary and provide varying levels of pollination services due to their relatively small size, hairiness (pilosity), and the masked bee group carrying pollen internally rather than packed onto the back leg (Donovan 2007). Considering introduced insect pollinators, specifically the honey bee (*Apis mellifera*) and the four naturalised bumblebee species (*Bombus* sp.), there is some evidence of increased pollination efficiency when compared to native solitary bees, as native bees are smaller, and not social nor hairy (Dohzono & Yokoyama 2010, Newstrom-Lloyd 2013). Social bees with the larger group of workers and ability to communicate around nectar and pollination sources more effectively provide pollination services when compared to solitary bees ((Dohzono & Yokoyama 2010). The extent of pollinator body hairiness, as best seen on introduced bumble bees, has been observed to increase likelihood of stigma contact and pollen carrying capacity (Stavert et al. 2016, Phillips et al. 2018, Woodcock et al. 2019). Overall, the hairy social bees brought and captively raised by humans have some positive impact on pollination services for native species, though it is not quantified; it is less efficient than bird pollination, and has unknown effect, though suggested as negative competition, on native insect species (Newstrom & Robertson 2005, Dohzono & Yokoyama 2010, Newstrom-Lloyd 2013). There appear to be continuing reduction in insect numbers worldwide with approximately

37% of insect species declining, especially in areas of high human population and/or high amounts of agricultural activity (Montgomery et al. 2020, Sánchez-Bayo 2021). Reliance on insect pollinators into the future will likely increase risk of pollination failure and increase chances of reduced seed production (van der Sluijs 2020).

1.3 Self-Compatibility, Inbreeding Depression, and Apomixis

A review of New Zealand plant species suggests that approximately 21% of species are self-incompatible and approximately 21% autonomously selfing (apomictic), leaving 58% of the species with mixed-mating strategies (Newstrom & Robertson 2005).

Kōwhai (*Sophora microphylla*) and kōtukutuku (*Fuschia excorticata*) are self-compatible yet suffer from extremely high inbreeding depression when genetic outcrossing is not available, with a potential 80% improvement in seed fitness to be gained from non-self pollination (Robertson et al. 2011, Etten et al. 2015). For Kōwhai populations suffering from inbreeding depression, almost half of seed produced were a genetic deadend, unable to reach a point of maturity where seed production occurred (Roberseon et al. 2011). This was despite the species being considered to have a typical amount of pollen limitation for a New Zealand tree species, highlighting that offspring resulting from such a depressed population can be markedly less viable with individual fitness reduced by a striking 96-99% when compared to outcrossed seedlings (Robertson et al. 2011). Similar filtering of low fitness progeny prior to maturity was also found in pōhutukawa (*Metrosideros excelsa*) and pūriri (*Vitex lucens*) as measured by significantly higher homozygosity and lower seedlings growth rates for self-pollinated seedlings (Barrell et al. 1997, Schmidt-Adam et al. 2000). This a problem in research projects, as this lowered fitness may not be immediately identified, a phenomenon termed “cryptic recruitment,” whereunder seedlings germinate and grow and are thus counted in initial experimental follow-up, but never reach sexual maturity themselves after conclusion of the experiment. The level of inbreeding depression impact can vary depending on species and is known to be particularly strong in long-lived species, and thus may potentially impact a wide variety of trees in New Zealand (Etten et al. 2015). For example, it is commonly believed that lone or small population kauri (*Agathis australis*) produce very few viable seeds, though the cause has not been confirmed as inbreeding depression (Metcalf 2007).

The effects of self-pollination and inbreeding depression likely pose a challenge for nurseries that collect seed from populations with a small number of individuals, whether found in the wild or in a cultivated scenario. This could lead to significant issues of seed supply in future due to lack of seedling survival.

Lack of self-compatibility requires multiple individuals for successful seed production and therefore germination. Lack of self-compatibility therefore prevents severely fragmented populations or specific individuals from contributing to the natural seed bank or regeneration rate of affected species. One of the most well-known self-incompatible species is rātā moehau (*Metrosideros bartlettii*), a critically endangered tree likely unable to produce seed without human intervention (van der Walt et al. 2022).

For New Zealand tree flora, monoecy (one tree with both male and female or hermaphroditic flowers on the same plant) is relatively rare with various forms of dioecy being relatively more common (separate trees having either male or female flowers only) (Webb & Kelly 1993, McGlone & Richardson 2023). Only 3.4% of tree flora are strictly monoecious (McGlone & Richardson 2023). Dioecious species require male and female individuals to be present for pollination to occur, increasing the risk of non-viable seed production for small or fragmented populations.

An alternative to self-compatible pollination in some species is autonomous selfing capability (apomixis), an asexual reproductive strategy in which female trees can produce viable seed without fertilisation (a phenomenon akin to parthenogenesis in the animal world). As the developed embryo does not undergo meiosis in apomictic reproduction, the negative effects of increasing homozygosity are avoided (Molloy 2019). While explicit proof of apomixis was previously restricted to genus *Coprosma* within the New Zealand flora, further potential functional apomixis has been indicated through observation of isolated female individuals in Riccarton Bush located in Christchurch (Heenan et al. 2002, Heenan et al. 2003, Molloy 2019). A possible benefit of apomictic reproduction relevant to seed collection and germination is the potential reduction in inbreeding depression, and thus improved viable seed production when compared with self-fertilising species. Collecting seed from healthy, yet isolated, female trees would not face the enormous fitness reductions previously encountered in self-fertilising species, though without the benefits of outcrossing being induced. The table below lists presumed indigenous apomictic trees

proposed thus far, though confirmation of this ability via cytology, progeny testing, or other DNA-based techniques is yet to be done (Molloy 2019). Apomixis is heritable yet controlled by epigenetics with progeny usually able to regress to sexual reproduction when outcrossing occurs (Grimanelli 2012, Höerandl & Hojsgaard 2012). Apomixis may also lead to range expansion and contribute to speciation over the long term (Höerandl & Hojsgaard 2012). Table 1 below lists proposed, yet unconfirmed, apomixis reproductive capability of tree species in New Zealand. This highlights potential species resistance to inbreeding depression and allows better decision making for seed collection and ability to determine standard germination outcomes.

Table 1: Potential facultative (rather than obligate) apomictic trees of New Zealand. Suggested by field observation (adapted from Molloy 2019).

Species	Adult Height	Isolated Female Sets Fruit
Tītoki - <i>Alectron excelsus</i> sub. <i>excelsus</i>	9m	Yes
Makomako - <i>Aristotelia serrata</i>	10m	No
Putaputawētā - <i>Carpodetus serratus</i>	10m	No
Karamū - <i>Coprosma robusta</i>	6m	No
Karaka - <i>Corynocarpus laevigatus</i>	15m	Yes
Kāpuka - <i>Griselinia littoralis</i>	15m	Yes
Porokaiwhiri - <i>Hedycaria arborea</i>	12m	No
Māhoe - <i>Melicytus ramiflorus</i>	15m	No
Puka - <i>Meryta sinclarii</i> -	8m	Yes
Red Matipo - <i>Myrsine australis</i>	6m	No
Kaikōmako - <i>Penantia corymbosa</i>	10m	No
Tarata - <i>Pittosporum eugenioides</i>	12m	No
Kōhūhū <i>Pittosporum tenuifolium</i>	10m	No
Mānatu - <i>Plagianthus regius</i> sub <i>regius</i>	15m	No
Whauwhaupaku - <i>Psuedopanax arboreus</i>	8m	No
Horoeka - <i>Psuedopanax crassifolius</i>	15m	No
Patē - <i>Schefflera digitata</i>	8m	No
Tūrepo - <i>Streblus heterophyllus</i>	12m	No

1.4 Maternal Effects versus Population Genetics

The environment in which the maternal plant grows has been shown to have some carryover viability effects on subsequent generations of plants. This is usually thought of as seeds receiving improved resource provisioning in good conditions, as generally determined by increased seed mass, or less often as increased seed vigour (Pico et al. 2004, Hereford & Moriuchi 2005, Bischoff et al. 2006, Bischoff & Müller-Schärer 2010). The improved seed quality from increased maternal resourcing is well-documented especially in stressful or competitive

environments as seen by higher seed viability and higher seedling survival (Sultan 1996, Donohue 1998, Riginos et al. 2007).

Adverse maternal conditions may also trigger responses which increase progeny survival by delaying germination (Philippi 1993). For a New Zealand native example, there is some suggestion of delayed seed maturation in response to lower maternal growing temperatures for hutu (*Ascarina lucida*) (Martin & Ogden 2002). Likewise, drought experienced by the maternal plant may produce seeds with thicker seed coats, increasing physical dormancy (Fenner & Thompson 2005, Liyanage & Ooi 2015). These maternal effects are somewhat similar to masting strategies as trees during masting years allocate more resources to reproduction than in other years. Physiological dormancy may also be decreased if maternal plants experience higher growing temperatures (Fenner 1991, Fenner & Thompson 2005, Liyanage & Ooi 2015) and amongst annual plants, parent plants grown in dry soil had offspring with reduced growth in dry soil (Waterman & Sultan 2021). This shows that the competitive conditions for parental plants can affect the variation and overall fitness of their offspring.

Large trees are also known to produce more seeds, though the assumed linear relationship between biomass and seed production did not hold true for Hall's tōtara (*Podocarpus laetus*), rimu (*Dacrydium cupressinum*), silver beech (*Lophozonia menziesii*), nor mountain beech (*Fuscospora cliffortioides*). The beeches did not increase relative reproductive efforts once a minimum size was reached. The conifers had a high minimum size for successful reproduction, with large trees dominating local seed creation (Canham et al. 2014).

The effects of genetics on germination across populations is well-known (Hernández-Verdugo et al. 2001, Baskin & Baskin 2015), and has been observed in New Zealand for hutu, pūriri, tarata (*Pittosporum eugenoides*), karo (*P. crassifolium*), and in the *Nothofagus* genus in Chile (same genus as Southern beech). Lowland hutu populations exhibited germination percentages of 32% vs 82% in higher altitude populations (Martin & Ogden 2002). At the southern part of its range, Pūriri exhibited significant differences in germination rates when comparing rural (Bushy Park) to urban populations (Victoria Lake, Whanganui) (Southward et al. 2002). Tarata seed collected in Palmerston North had significantly lower germination percentages (approximately 30%) when compared to seed collected in Wellington (93%) which also had significantly higher seed moisture content upon collection (Kai et al. 2023). Germination percentage was higher for karo seed collected from Palmerston North in comparison to Wellington (75% vs 53%) despite no difference in seed moisture content (Kai et al. 2023). *Fuscospora* (formerly *Nothofagus*) species seem to follow the rules of larger seed mass equating to higher germination percentage, as well as decreasing seed viability and seed amount produced by higher elevation populations (Ogden 1985, Moya et al. 2017).

Overall, there is still uncertainty in the published literature around the relative strength of maternal effects versus population genetics on germination percentages and rates. These are two powerful factors to explore further to improve seed collection practices for improved seed viability, germination rates, and seedling success. Recording the germination rates and percentages from specific seed collections will assist in building a valuable database for these comparisons, as well as identifying particularly viable or problematic seed parent populations.

1.5 Masting, Dispersal, and Seed Banks

Masting as a seed production strategy is relatively common in New Zealand in both woody and non-woody plant species (Webb & Kelly 1993). Pulsed seed production is most well known in the beech-dominated forest, where it has significant repercussions for the populations of invasive mammals (Kelly et al. 2008). There is evidence that in years of high seed production, germination rates of seed are also marginally higher, though in the southern beech group there is more variation in germination rates based on genetic provenance or population location (Beggs 1999, Burns 2012, Santelices et al. 2017). There is evidence that this improvement in germination in mast years is due to increased pollination efficiency (Kelly et al. 2001). Masting also has been shown to improve dispersal rates, which itself improves germination in certain species, though this phenomenon has not been observed specifically for New Zealand tall tree species. Kohekohe (*Didymocheton spectabilis*, formerly *Dysoxylum spectabile*) masting was predicted by higher rainfall amounts rather than temperature (which is the predictor for southern beech species) (Webb 2018). Mast-year seed showed non-significantly higher germination percentage when compared to non-mast-year seed (80% vs 60%) but significantly higher survivorship after 2 years (60% vs 0%), which emphasises the sensitivity of kohekohe recruitment to moist conditions (Burns 2012). Further understanding of mast seeding events

can inform timings of: species reintroductions, culling activity, selective harvesting (gap creation), population viability assessments, zoonotic disease forecasting, and seed collection for tree production or human use. (Pearse et al. 2021). So, while masting impacts on germination for New Zealand woody species are mixed, there is still room for further research to explore this impact on the wider list of masting species given the suggestion of germination improvement.

Table 2: List of Masting and Non-Masting Tree Species (Webb & Kelly 1993, Schaubert et al. 2002, Burns 2012, Webb 2018)

Masting Species	
Scientific Name	Common Name
<i>Hoheria sp.</i>	Hungere, Houhere, Whauwhi, Houhi
<i>Didymocheton spectabilis</i>	Kohekohe
<i>Elaeocarpus dentatus</i>	Hīnau
<i>Ixerba brexioides</i>	Tawari
<i>Phyllocladus trichomanoides</i>	Tanekaha
<i>Lophozonia menziesii</i>	Silver Beech
<i>Fuscospora fusca</i>	Red Beech
<i>Fuscospora cliffortioides</i>	Mountain Beech
<i>Fuscospora truncata</i>	Hard Beech
<i>Dacrycarpus dacrydioides</i>	Kahikatea
<i>Dacrydium cupressinum</i>	Rimu
<i>Prumnopitys taxifolia</i>	Mataī
Non-Masting Species	
Scientific Name	Common Name
<i>Melicytus ramiflorus</i>	Māhoe
<i>Podocarpus totara</i>	Tōtara
<i>Corynocarpus laevigatus</i>	Karaka
<i>Pittosporum sp.</i>	Tarata, Kōhūhū, Karo, Haekaro
<i>Pectinopitys ferruginea</i>	Miro
<i>Podocarpus acutifolius</i>	Needle-Leaved Tōtara

1.6 Seed Dispersal

Seed dispersal significantly impacts germination success, manifesting through mechanisms such as: seed ingestion breaking dormancy, avoidance of allelopathic effects under conspecifics, and strategic placement in favourable microsites. Understanding of particular dispersal mechanisms can inform the development of germination protocols (e.g. removal of fleshy fruit, a proxy for frugivore digestion and dispersal, to speed germination rate). The Seed Dispersal Effectiveness framework (SDE), as proposed by Schupp (1993) and further elaborated by Schupp et al. (2010), provides structure to our current understanding of the interaction of seed dispersal on successful plant recruitment. Quantitative aspects of SDE include the number of seeds consumed and dispersed, while the qualitative aspects include dispersal distance, location, the effects of gut passage and other traits of the dispersal agent (Schupp 1993). Various types of short-range dispersal strategies focus seeds to nearby locations for population permanence rather than focusing on individual plant success. This restricts dispersal to the established parent plant patch; in other words, to an area with demonstrable survival success for that species (Pufal & Garnock-Jones 2010). The initial seed movement phase, called primary dispersal, involves the initial transportation of seed-bearing fruit away from the parent plant. This process holds importance in enhancing viability and germination rates while also shaping the species' range and distribution (Estrada & Fleming 2012). Moreover,

broader primary dispersal serves to mitigate density-dependent mortality resulting from intraspecific competition and specialised ecological competitors which exist under the parent canopy.

New Zealand flora is unique in the fact that many of its woody species have a higher relative number of fleshy-fruited species, as well as a higher proportion of such species inhabiting alpine regions when compared to global species assemblages. This prevalence in alpine regions is suggestive of the importance of animals acting as dispersers (Burrows 1994b, Lord 1999, Kelly et al. 2010). Only 5.5% of New Zealand tree species are wind dispersed while approximately 70% are reliant on animal dispersers (Burrows 1994b). New Zealand also has one of the highest proportions of attachment-dispersed genera, though many of these plant species are now at risk of extinction given the dramatic reduction in flightless bird species now present (de Lange et al. 2004, Thorsen et al. 2009). Another unique aspect of New Zealand dispersal ecology is the co-evolution of seed dispersal with avian and reptile fauna rather than mammalian species; these being usually classified into three groups (1) flightless birds - mostly extinct and relatively large, (2) flighted or volant birds - extinct and extant, native and non-native, and (3) lizards - who are relatively understudied as dispersal agents (Lord et al. 2002). These dispersal mutualisms have significantly changed following the arrival of humans and subsequent increases in mammalian populations in modern New Zealand. Changes in bird populations and behaviour can cause functional loss of this process even with dispersers still present in the environment (McConkey & O'Farrill 2016), with impacts including changes to germination patterns, seed shadows, deposition of seeds to unsuitable microsites, and different rates of consumption (Traveset & Richardson 2006, Westphal 2019).

Of New Zealand indigenous animals, both extinct and extant species, 114 species of reptile and bird contained fruit in their diet, acting as seed dispersal agents. Only 13 species (6% of terrestrial fauna) are considered predominantly frugivorous (Thorsen et al. 2011). These 114 species were responsible for the dispersal of 329 fleshy-fruited flora (13.6% of plant species) (Thorsen et al. 2009). There are 11 extant native bird species that are considered frugivorous including kereru (*Hemiphaga novaeseelandiae*), parea (*Hemiphaga chathamensis*), bellbird (*Anthornis melanura*), silvereye (*Zosterops lateralis*), tui (*Prosthemadera novaeseelandiae*) and stitchbird (*Notiomystis cincta*), kokako (*Callaeas wilsoni*), both the North and South Island saddleback (*Philesturnus rufusater* and *P. carunculatus*), brown kiwi (*Apteryx mantelli*), and weka (*Gallirallus australis*). There are a further nine species which consume some fruit, these being: rifleman (*Acanthisitta chloris*), fantail (*Rhipidura fuliginosa*), yellowhead (*Mohoua ochrocephala*), whitehead (*Mohoua albicilla*), brown creeper (*Mohoua novaeseelandiae*), grey warbler (*Gerygone igata*), tomtit (*Petroica macrocephala*), the New Zealand robin (*Petroica australis*), and both the red and yellow crowned parakeet (*Cyanoramphus novaezelandia*, *C. auriceps*) (Dawson & Lucas 2000).

The kereru is the only extant indigenous species capable of dispersing fruits larger than 15mm in diameter, thus affecting five tree species: tawa (*Beilschmiedia tawa*), taraire (*Beilschmiedia tarairi*), pūriri, karaka (*Corynocarpus laevigatus*), and tawapou (*Planchonella costata*). These large seeds seemingly evolved for very slow germination, which may have been advantageous in the low disturbance forest of pre-human occupied New Zealand. It should be noted that the now extinct moa species did not disperse large seeds, as was previously thought. (Carpenter et al. 2018). While large seeds were present in the gizzard, no seeds larger than 3.3mm were found in the fossilised faeces of moa, as all food was finely ground by powerful gizzard pressure which has no analogy to extant ratites such as emu (Carpenter et al. 2018).

However, New Zealand flora is now thought of as less dependent on frugivores than previously considered, and evidence that many large-fruited species still receive sufficient dispersal services (Kelly et al. 2010, Wyman 2013). None of the 19 species tested for dependency showed consistent failure of germination when comparing between cleaned seeds and whole fruit (Kelly et al. 2010). Further evidence is the extinction of only three plant species despite 40% of terrestrial avifauna having gone extinct since human residency (Atkinson & Milener 1991, Sax et al. 2002). Though New Zealand seems lacking in obligate avian frugivore dispersal relationships, there can still be non-extinction level impacts on plant populations due to lack of dispersal.

A study of both taraire and karaka, two species thought to have reduced dispersal due to loss of appropriate frugivores as well as minimal dispersal replacement by introduced mammals, found significantly reduced germination and survival over the first two years of study (Wotton & Kelly 2011). For karaka, seed movement away from the seed parent created the largest impact on increased germination due to lower seed predation, while taraire germination was improved by both fruit removal and distance from the parent tree (Wotton 2007, Wotton & Kelly

2011, Morales et al. 2014). This result shows the positive impact of dispersal itself on germination and survival for karaka, with dispersal agent ingestion or fruit removal by hand acting as additional important factors in improving taraire germination. Interestingly in a controlled germination experiment, taraire also increased germination success when whole fruit was sown at high density, potentially due to the anti-fungal jelly secreted by the seeds, while fruit removal increased overall seedling survival in natural environments over the long-term (Myers 1984, Wotton & Kelly 2011). Weka (*Gallirallus australis*) have the possibility of being important seed dispersers, with 93-96% of miro (*Pectinopitys ferruginea*, formerly *Prumnopitys f.*) and hīnau seeds being dispersed away from seed parent canopies and approximately 1% being dispersed further than 1 km (Carpenter et al. 2019). Native bird dispersers in the alpine areas of New Zealand are now restricted to a small number of species, including kea (*Nestor notabilis*) as the most important, along with occasional dispersal events by pipit (*Anthus novaeseelandiae*) (Clarke 1971, Young 2012), falcon (*Falco novaeseelandiae*) (Young & Bell, 2010), rock wren (*Xenicus gilviventris*), and rare visits from forest birds.

Lizards are known to consume the seeds of 23 native species, though this effort is focused mainly on shrubs and divaricating species with white-blue fruited species (Lord & Marshall 2001, Wotton et al. 2016). In terms of seed quantity, lizards have been shown to remove a significant portion of available seeds, sometimes showing no increase in amounts removed when birds also had plant access, emphasising similar potential capability (Wotton 2002). While seeds were usually dispersed less than 20 m from the seed parent this can still be far enough to escape the adult canopy and associated negative germination effects (Wotton et al. 2016). In the South Island subalpine habitat, lizards accounted for approximately 50% of all fruits removed by frugivores (Young & Kelly 2014). Tree seeds eaten by lizards are: Taupata (*Coprosma repens*) eaten by the shore skink (*Oligosoma smithi*) and the spotted skink (*O. lineoocellatum*) (Whitaker 1987, Higgins et al. 2006, Wotton et al. 2016); Karamu eaten by the spotted skink and northern grass skink (*O. polychroma*) (Williams & Karl 1996, Wotton et al. 2016); Kawakawa is eaten by Duvaucel's gecko (*Hoplodactylus duvaucelii*), Poor Knight's Geckos (*Dactylocnemis 'Poor Knights'*), the marbled skink (*O. oliveri*), the robust skin (*O. alani*), Whitaker's skink (*O. whitakeri*), the shore skink, and the Raukawa gecko (*Woodworthia maculata*) (Whitaker 1968, Wotton et al. 2016); and ngaio eaten by the Three Kings skink (*O. fallai*) (Parrish & Gill 2003, Higgins et al. 2006).

There is significant evidence that introduced mammals are acting as seed dispersal agents in both lowland and alpine environments (Young 2012, O'Connor & Kelly 2012, Parkes et al. 2015, Dickinson 2021). Seed suitable for this endozoochory would likely need to be small and hard-coated to avoid chewing damage and for resistance to digestion, thus enabling seeds to be able to pass through the ungulate while maintaining germination viability. (Bellingham & Lee 2006). Kāpuka seed has been found in the rumen of red deer (*Cervus elaphus*) (Forsyth et al. 2010).

Pigs are known to disperse mataī, miro and hīnau (*Elaeocarpus dentatus*) fruit (O'Connor & Kelly, Parkes et al. 2015). 14% of mataī seeds were proven to pass through the gut of two domestic kunekune pigs with 57% of these domestically digested seeds germinated under glasshouse conditions which is comparable to hand-cleaned seed (O'Connor & Kelly 2012). Of 450 intact mataī seeds collected from 3.5kg of wild pig faeces in Marlborough, 68% germination percentage was reached after 22 months. With pigs possibly travelling several kilometres in a 24-hour period and a gut passage time of 2-4 days, they likely are important for long-distance dispersal of native and invasive species in New Zealand (O'Connor & Kelly 2012). Feral pigs (*sus scrofa*) were also shown to disperse 2.2% of seeds at alpine sites, with a median dispersal distance of 0.5 - 2km.

In the alpine context, possums (*Trichosurus vulpecula*) are the most numerically important animal seed dispersers and were the only recorded dispersers for beech species. Possums often moved beech seeds into forest areas which provided higher levels of suitable germination sites, with shade being an important factor for germination success for alpine species. They damaged 3.4% of seeds which passed through their gut (Young 2012). Continuing in the alpine environment, lagomorphs were found to disperse 13% of seeds, with hedgehogs dispersing a further 3.2% of seeds (Young 2012).

Part 1: Knowledge Gaps

1. The specific impacts of pollen limitation on seed production and seed vigour. Does less pollen landing on the stigma of native trees reduce the viability, or other traits, of seed?

2. The quantification of native and non-native insect pollination for native tree seed production. How has the influx of managed bee colonies affected native pollinator populations? Has there been any reductions in insect pollinator effectiveness due to changing population sizes or competition?
3. The impacts of mast seeding resource allocation on germination capability for a wider range of native tree species. What are the differences in individual seed mass, seed numbers, seed maturation rate, and viability when comparing seed produced in masting years to seed produced in non-masting years?
4. The effects of maternal plant growing conditions on progeny viability are unstudied in New Zealand native trees beyond two examples. Can seed parents be better managed or cared for to produce higher quality seed and higher progeny? What management decisions will make the most impact on seed quality?

2. Seed Dormancy and Germination Inhibition

Consistent and high germination percentages and rates allow for predictable seedlings production in a nursery system. Alleviation of dormancy, in those species which exhibit dormancy, is a critical step to creating efficient and dependable seedling volume ready for use in the native afforestation industry. This section aims to explore dormancy function in New Zealand native trees with the potential to apply new knowledge to the science of germination.

A seed is considered dormant if it does not germinate in a specific time frame when experiencing environmental conditions that are otherwise favourable to its development (Baskin & Baskin 2004a). Seed dormancy evolved to avoid vulnerable seedlings germinating during adverse ephemeral or transient environmental conditions. Alleviating dormancy is a major factor in promoting germination, as the process of breaking dormancy can be complicated, and, depending on the type of dormancy, one requiring varying temperature treatments, mechanical scarification, and/or certain storage conditions to overcome the dormancy barrier.

Theoretical models postulate that No Dormancy (ND) represents an evolutionarily stable strategy in environments that have relatively unchanging conditions, for example a tropical rainforest which does not have seasonal changes (Rees 1996). In contrast, seed dormancy, characterised as a highly heritable and phylogenetically conserved trait (Donohue et al. 2010, Wagmann et al. 2012, Dayrell et al. 2017), is favoured in less predictable or more intermittently disturbed environments such as those affected by fires (Venable & Brown 1988, Philippi 1993, Pausas & Keeley 2014, Dayrell et al. 2017). According to the dormancy classification system outlined by Baskin and Baskin (2004b) and reviewed by Finch-Savage and Leubner Metzger (2006), seed dormancy can be categorised broadly into five types: (a) physical dormancy (PY), characterised by seeds featuring an impermeable coat impeding water access to the embryo; (b) physiological dormancy (PD), involving aspects of the embryo or surrounding endosperm tissues; (c) morphological dormancy (MD), where the embryo is underdeveloped at dispersal and necessitates a period for additional growth; (d) morphophysiological dormancy (MPD), where the embryo remains undeveloped due to hormonal imbalances inhibiting further growth and germination; and (e) combinational dormancy (PY+PD), wherein seeds demonstrate both a physical water barrier and physiological dormancy. For detailed insights into the underlying mechanisms of these commonly occurring dormancy types, comprehensive reviews are available for physical dormancy (Baskin & Baskin 2004b) and physiological dormancy (Finch-Savage & Leubner Metzger 2006, Finkelstein et al. 2008). Numerous studies have been conducted to address seed dormancy removal, with specific strategies contingent upon the particular type of seed dormancy in question. Seed dormancy, or lack thereof, as found in New Zealand tree species is discussed below.

See Appendix 2 for list of New Zealand Tree families and supposed dormancy classes.

2.1 No Dormancy

These seeds germinate rapidly when exposed to the correct environmental conditions (Baskin & Baskin 2004a). By promoting rapid germination ND may increase competitive advantage, lengthen the growing period, or decrease generation turnover time (Willis et al. 2014, Zhang et al. 2022). ND may also be favoured during colonisation of novel environments because of the lack of restrictions on germination (Willis et al. 2014). Of the tree and shrub plant families found in New Zealand, this is the second most common seed state. For this group of plants, sowing of fresh seed is essential for germination success. The timing and coordination of seed collections with nursery capacity and operation is also important to consider for seedling production.

Potential species of interest: Kauri (*Agathis australis*), manawa, mangrove (*Avicennia marina subsp. australasica*), tutu (*Coriaria arborea var. arborea*), kāpuka (*Griselinia littoralis*), puka (*G. lucida*), kānuka (*Kunzea sp.*), mānuka (*Leptospermum scoparium*), ramarama (*Lophomyrtys sp.*), rātā (*Metrosideros sp.*), rōhutu (*Neomyrtus pedunculata*), Swamp maire (*Syzygium maire*), kōtukutuku, kawakawa (*Piper sp.*).

2.2 Physical Dormancy

Globally, 18 plant families are known to exhibit physical dormancy (PY), which makes it a relatively rare dormancy type (Baskin 2003, Baskin et al. 2006, Jayasuriya et al. 2010, Gama-Arachchige et al. 2010, Gama-Arachchige et al. 2013). For seeds with PY, germination cannot occur until the seed or fruit coat becomes permeable to water (Baskin et al. 2000). When the dormancy is broken, water is taken in by the seed through a specialised region known as the “water gap” or “water gap complex”. Across the taxonomic groups there are significant differences in the anatomical structure of the water gap and its relationship to the remainder of the seed coat (Erickson et al. 2016). In particular, Lauraceae, which includes tawa, taraire, and mangeao tree species, has not yet been described.

Temperature has been shown to be the dominant controlling influence of water gap opening, though in some circumstances moisture also drives the change (Auld & O’Connell 1991, Burrows et al. 2009, Santana et al. 2010, de Paula et al. 2012, Gama-Arachchige et al. 2013). It is thought that temperature control allows the seed to “sense” favourable conditions and allows the seed coat to become permeable at the most appropriate time for seedling development (Jayasuriya et al. 2009, Gama-Arachchige et al. 2013). Once imbibition occurs, germination is usually rapid and will occur across a wide range of temperatures (Baskin 2003). The relevant 4 woody plant families in New Zealand are discussed below.

Physical dormancy was the last dormancy type to evolve and the negative diversification rates of PY species suggest that PY is limited in its capacity to diversify evolutionarily. One hypothesis to explain this limitation is that PY is not simply an adaptation to control germination but might also be under selection as a physical protection against pathogens and predators (Dalling et al. 2011, Paulsen et al. 2013).

a. Fabaceae - (kākābeak (*Clianthus* sp.), kōwhai)

Species in Fabaceae likely have a lens-like water gap complex. This structure suggests some seasonal sensitivity around breaking of dormancy as the cellular structure of the water gap may open and then revert to dormancy after a small amount of water absorption. This PY with sensitivity is considered the most highly evolved angiosperm dormancy type to avoid germinating out of season while maintaining a long-lived seed bank if sufficiently triggering conditions are not met (Jayasuriya et al. 2009).

Fabaceae species in fire-prone habitat have shown variable germination response to temperature variability, thought to assist in winder population persistence as a ‘bet-hedging’ strategy when encountering a range of soil heating (Liyanage & Ooi 2015). In breaking PY in the natural seed bank, there is evidence of bacteria and/or fungi acting via microbial scarification, with some soil community species also releasing germination promoting hormones (i.e. gibberellin) (Wu et al. 2023). Drought experienced by the maternal plant may produce seeds with thicker seed coats, which can increase the degree of PY (Nooden et al. 1985, Fenner & Thompson 2005, Liyanage & Ooi 2015). Many different protocols have been developed for breaking PY for controlled germination. Hot water and/or sulfuric acid soaking, and dry heat have all been shown to improve germination, though species-specific protocols are required to avoid unnecessary seed damage and death (Erickson et al. 2016). Both kakabeak and kōwhai have been shown to improve germination with boiling water treatments.

b. Malvaceae - (whau (*Entelea arborescens*), houhere/lacebark (*Hoheria* sp.), manatu/ribbonwood (*Plagianthus* sp.))

Species in this genera likely have a cap-in-plug water gap complex. This suggests no seasonal sensitivity to temperature, but rather an irreversible water permeability once dormancy is broken (Gama-Arachchige et al. 2013).

c. Sapindaceae - (Tītoki (*Alectron excelsus* subs. *excelsus*), Akeake (*Dodonaea viscosa*))

Akeake has been shown to germinate more quickly with mechanical scarification than a hot water treatment (germination in 1 to 5 days rather than 12 to 14) and was not shown to revert to dormancy after PY was initially broken. Akeake has shown signs of seasonal temperature sensitivity with warm storage for 32 weeks at 35°C unable to break dormancy, while water treatment above 80°C for 30 seconds resulted in successful alleviation (Jaganathan & Liu 2014). This type of temperature fluctuation would likely be achieved in the top layers of soil over the summer

period. Burying seeds for 2 years increased germination from 7 to 71%, thus suggesting that high summer soil temperatures ‘pre-conditioned’ the seeds to break dormancy (Jaganathan & Liu 2014).

d. Rhamnaceae - (Kumerahou (*Pomederris* sp.), Matagouri (*Discaria* sp.))

For Rhamnaceae, hot water treatment of seeds has been shown to improve germination with temperature and germination increased up to a certain peak. A temperature of 70-90°C is recommended to achieve high germination and avoid the potential seed damage and subsequent drop in germination that can occur above 100°C. It appears that once a specific temperature is reached, dormancy is likely broken regardless of exposure time, with a 2-5 min treatment being sufficient. This rise and peak in germination is not as pronounced with dry heat treatments, which can take more time and higher temperatures to be effective (Erickson et al 2016).

2.3 Physiological Dormancy

Physiological dormancy (PD) is the most common dormancy type globally and is likely to be the most common dormancy type in New Zealand trees (Baskin & Baskin 2004a, 2014). Physiological dormancy encompasses a wide range of physiological responses to environmental factors, such as temperature, light, gas concentrations (carbon dioxide, oxygen), and water (Finch-Savage & Leubner-Metzger 2006). There is an identified trend of maternal plants that experience higher growing temperatures decrease physiological dormancy of their progeny (Wood et al. 1980, Fenner 1991, Fenner & Thompson 2005, Liyanage & Ooi 2015). This may suggest that as global and local temperatures fluctuate with climate change, there will be a trend of increased germination percentage possibility for seed collected in hot years.

There are two classes of PD, regular and epicotyl. In regular PD, the root and shoot emerge within several days of each other once germination has begun. In epicotyl PD, there is a delay of 1-3 months between root and shoot emergence (Baskin & Baskin 2021). There are also several depths of PD (nondeep, intermediate, deep) which have some correlation to embryonic shape, size, and development (Soltani et al. 2017, Baskin & Baskin 2022). Overall, PD is usually broken by cycles of warm and cold stratification, the order of which can be hypothesised for individual species by examining when seed ripens and when germination occurs (Baskin & Baskin 2022). Conducting a “move-along” experiment (as described in Baskin & Baskin 2004a and reviewed in Baskin & Baskin 2022) can assist in detecting the necessary temperature regimes for breaking PD for unstudied species with low seed availability.

Some species do germinate more readily when the fleshy pulp of the fruit is removed (known as the deinhibition effect), though removal by frugivore digestion does not show an increase in germination outcome when compared to artificial or hand removal (Robertson et al. 2006). Previous germination studies by C.J. Burrows in the 1990s showed that fruit removal significantly sped up germination for a variety of native trees. However, this was later found to be an artefact of experimental conditions, specifically the use of petri dishes preventing leaching activity, and since has been revisited and disproven for several fleshy fruited species including karaka and tawa (Robertson et al. 2006, Kelly et al. 2009).

For many of the New Zealand species listed below they are known to engage in significantly long (>2years) dormancy periods. In particular hīnau and pōkākā are known as difficult to germinate. Currently there is little published information in the literature around alleviation of dormancy for these species.

Potential species of interest: pāhautea (*Libocedrus bidwillii*), kawaka (*Libocedrus plumosa*), tree daisies (*Olearia* sp.), taraire, tawa, mangeao (*Litsea calicaris*), kāmahī/towai (*Pterophylla* (formerly *Weinmannia*) *racemosa/sylvicola*), makomako (*Aristotelia serrata*), mountain wineberry (*A. frutosa*), hīnau, pōkākā (*Elaeocarpus hookerianus*), *Dracophyllum* sp., Kermadec poplar (*Homalanthus polyandrus*), pūriri, hangehange (*Geniostoma* sp.) Southern beeches, parapara (*Ceodes brunoniana*), maire (*Nestegis* sp.), matipo (*Myrsine* sp.), rewarewa (*Knightia excelsa*), toru (*Toronia toru*), *Coprosma* sp., wharangi (*Melicope ternata*), tītoki, ngaio (*Myoporum laetum*), poroporo (*Solanum* sp.), māhoe (*Melicytus* sp.).

2.4 Morphological Dormancy

Morphological dormancy is dictated by the underdevelopment of the embryo within the seed (Baskin & Baskin 2003b, 2004b, 2014). This means that the embryo requires a period of time for the tissues to differentiate or grow to sufficient size before germination can occur (Baskin & Baskin 2003b). In practice, these seeds do not require any specialised treatments to allow embryo maturation, which usually occurs within 30 days of dispersal (Finch-Savage & Leubner-Metzger 2006, Baskin & Baskin 2014). Embryonic underdevelopment is most likely to be the ancestral form of seed dormancy in seed producing species (Baskin & Baskin 2014, Willis et al. 2014).

Potential species of interest: *rauakaua* genus, patē (*schefflera digitata*), *pittosporum* genus, and some podocarps.

2.5 Morphophysiological Dormancy

MPD is related to embryonic development as controlled by hormone secretion and is the third most common dormancy type found in New Zealand. The embryos are also underdeveloped similarly to MD, but further development has hormonal control in place (Baskin & Baskin 2004b, Finch-Savage & Leubner-Metzger 2006). The “classical” groups of plant hormones are the auxins, gibberellins (GA), cytokinins, abscisic acid (ABA), and ethylene; with more recent considerations of, brassinosteroids, jasmonates (JA), and strigolactones as important germination factors (Davis 2009, Rademacher 2015, Kazan & Lyons 2016). Two major plant hormones, ABA and GA, are both common to all seed plants and play a central role in dormancy regulation (Rademacher 2015). Heavy metals also affect hormones in the germination process. A negative correlation has also been observed between gibberellic acid and cytokinins in chickpea seeds germinating at low cadmium concentrations (Atici et al. 2005). Similar reports on the inhibitory and toxic effects of lead on seed germination and endogenous chemical compounds other crops as *Oryza sativa* (Hsu & Kao 2003, Jayakumar et al. 2008), *Sinapis alba* (Fargasova 1994), *Sonchus oleraceus* (Xiong 1998a), and *Brassica pekinensis* (Xiong 1998b).

GAs are the most well-studied category of the plant hormones relating to germination regulation and they have a wide range of activity relating to plant growth (Rowarth et al. 2007). This group of hormones are designated by GAn, where the ‘n’ defines the order of discovery (Hill 1977, Arteca 1995). The main hormonal functions of GAs in higher plants are the promotion of longitudinal growth, the induction of hydrolytic enzymes in germinating seeds, the induction of bolting in long-day plants, and the promotion of fruit setting and development. ABA plays a major role in protecting higher plants against abiotic stress. It leads to stomatal closure, when plants are under drought stress and increases cold hardiness of plant tissues. Another function of ABA is its involvement in inhibiting precocious seed germination. Induction and maintenance of seed dormancy by abscisic acid (ABA) and dormancy release by gibberellin (GA) are observed in many species (Nonogaki 2019). In the germination timeline GA and ABA negatively regulate each other with GA production ramping when ABA decreases and vice versa, with exact timelines of this interaction are likely concurrent and/or species specific (Nonogaki et al. 2014, Nonogaki 2019).

It has been shown that high levels of GA₃ have been shown as beneficial to male cone production across several conifers including *Pinus* (Niu et al. 2014) and Douglas Fir (*Pseudotsuga menziesii*) (Kong et al. 2008). The aforementioned studies led to an exploration in the genus *Dacrydium* (as seen in New Zealand native Rimu), which instead showed fluctuations in JAs as connected with cone maturation (Lu et al. 2020). In Norway Spruce (*Picea abies*) auxins were measured at a maximum during embryo maturation, with JAs reappearing in peak concentration during the germination phase (Vondrakova 2018). These studies suggest that the hormonal pathway of germination for conifer species is different than for angiosperms, with potential unique research outcomes for New Zealand species given our unique set of gymnosperms.

Auxin also appeared in embryo maturation in Tamarillo (genus *Solanum*, as seen in New Zealand native Poroporo species, *S. aviculare*, *S. lacinatum*), playing a key role in the bilateral symmetry of the embryo development and for germination (Caeiro et al. 2022). At point of writing this review, no further published information is available that is specific to New Zealand tree species.

Potential species of interest: some Podocarps, *pseudopanax* sp., *rauakaua* genus, patē, puka, pukatea (*Laurelia novae-zelandiae*), tūrepo (*Streblus* sp.), tāwari (*Ixerba brexioides*), horopito (*Pseudowintera* sp.), nīkau

(*Rhopalostylis sapida*), tī kōuka (*cordyline* sp.), hutu, karaka, porokaiwhiri (*Hedycaria arborea*), *Pittosporum* sp., putaputawētā (*Carpodetus serratus*).

Table 3: Methods currently used to break dormancy for New Zealand native trees. If a germination protocol is unknown, these techniques are known to be effective and should be first explored (Hill 2004).

Name	Methodology	Example species
Water soaking	Soak seeds in room temperature water for 24-48. This removes any water-soluble germination inhibitors.	Horoeke, māhoe
Hot water soaking	Bring water to a boil, add seeds and remove from heat. Allow to cool fully. This can address both PY and PD.	Kōwhai, puriri
Acid Treatment	Immerse seeds in concentrated sulfuric acid for 15-30 min, then wash under running water for 10min to remove any remaining acid. CAUTION - note that acid is added to water (NOT water to acid) and personal protective equipment is required	Kōwhai
Physical scarification	Breaking or cracking the seed coat. Nicking with clippers or a knife, sandpaper abrasion, tumbling the seed in a sandpaper lined mixing tub. Successful abrasion is testing by putting a sample of seed in water overnight to note if imbibition/expansion occurs. If not, repeat the process.	Whao, akeake, tainui, puriri
Stratification	Refrigeration of soaked seeds at 4-5°C for some number of weeks or months. This allows imbibition to occur and germination enzymes to become active.	Tī kōuka, ngaio, southern beech species.
Incubation + Stratification	Seeds kept warm and dry for 1-3 months, then followed by cold stratification.	Kawakawa
Chemical priming	Seed is soaking in 1% H ₂ O ₂ solution then placed on blotting paper to germinate. Could also use 0.05 GA, or KNO ₃ (0.2% solution).	Unknown
Light	Seeds are exposed to light during germination.	mānuka, karamu, putaputaweta, pokaiwhiri, puriri
Washing seed	Seeds are washed in running water for at least 6 hours to remove water soluble germination inhibitors.	Māhoe
Alternative Temperatures	Expose seeds to fluctuating temperatures throughout germination, such as 20°C at night, 30 during day.	Unknown
Peeling Seed	Removal of seed capsule and/or fleshy fruit also removes germination inhibition. Similar to digestion by dispersing animals.	Rimu, kāpuka, miro, <i>Pseudopanax</i> sp.

2.6 Combination Dormancy (PY + PD)

Combination dormancy involves both a hard seed coat alongside some kind of physiological response factors. In real world situations, this is somewhat similar to seasonal PY. In the natural seed bank, there is evidence of bacteria and fungi acting via microbial scarification, with some species also releasing germination promoting hormones (i.e. gibberellin) (Wu et al. 2023). Microbial scarification alongside soil moisture is likely the natural mechanism for breaking dormancy in seeds with combination dormancy (Baskin & Baskin 2014).

Part 2: Knowledge Gaps

1. Outside of ND and PY seeds, clarification is needed around correct dormancy classes for native tree seeds. What levels of embryo development are present in mature seed of different species? Are there more tree species that would benefit from hot-cold stratification treatments rather than cool-moist stratification only?
2. Hormone fluctuations in native tree seeds during germination are essentially unknown though general hormonal fluctuations of both GA and ABA have been studied in crop species. What hormone fluctuations happen at what point for tree seeds? Which hormones could be used in nursery settings to break dormancy?

3. Seed Production and Germination in Nature

This section will explore the impacts of various abiotic and biotic conditions which have been shown to affect germination of New Zealand native trees. Certainly, there are tree species in New Zealand which are known to readily self-seed, such as tī kōuka, *hoheria* sp., mānuka, kānuka, and akeake. Māhoe, *Pittosporum* species, and poroporo can show up unannounced on occasion alongside kōwhai, which needs to be pricked out if the seedlings are to survive (Hill 2004). Examination of the environmental factors creates the wider context of seed production and tree recruitment in nature and provides information to better inform germination activities for commercial production. There is also importance in managing the remaining native forest to increase seed supply. This section also aims to be useful to land managers and owners who want to increase chances of native revegetation through pest and weed management decisions, evaluate the risks and opportunities of certain sites to follow native species succession, and better understand the influential players in the ecosystem around seed production to achieve native tall tree afforestation.

3.1 Climate Change and Other Human Influences

Climate change has and will continue to be an important driver of New Zealand's unique evolutionary and ecological history (McGlone et al. 2010, Macinnis-Ng et al. 2021). Projections of average surface temperature warming of 2.1°C by 2090 relative to 1980-99 (Lundquist et al. 2011). Projected annual mean precipitation changes suggest up to a 5% increase in the west by 2040, and 10% by 2090, and decreases in the east and north, sometimes exceeding 5% by 2090, driven by increased westerly winds in winter and spring (Ministry for the Environment 2008). And also, rainfall is likely to be more spatially/seasonally variable. Climate change also predicts increasing risks of fire and strong weather events which are also discussed below.

In New Zealand, changes in the distribution and composition of native forest are expected to follow the changes in rainfall, increasing westerly winds, and higher temperatures (Hennessy et al. 2007, Lundquist et al. 2011). Fragmented and isolated populations are presumed to be less resilient to climate change and increase likelihood of the seed production risks mentioned in the first section. This fragmentation potentially increases as species are forced to change distribution to higher altitudes. As an example of this, native mangroves are predicted to extend southward (Morrissey et al. 2010, Lundquist et al. 2014). As atmospheric CO₂ also increases, this will likely have cascading effects on nutrient cycling in all types of aquatic and terrestrial ecosystems (McGlone et al. 2010). Higher amounts of CO₂ are expected to increase plant growth as the higher carbon concentration accelerates rates of photosynthesis for most plants (Lovelock 2008, Gamage et al. 2018). While information specific to seed germination is lacking, faster growth rates may benefit seedlings, accelerating them through their first fragile stages of growth or act as a negative interaction marking increased competition for space and other growth inputs.

For seed production, masting schedules are likely to be impacted, with the interannual cycles of temperature changing as well as stored plant resources being affected by seasonal factors (Schauber et al. 2002, Monks et al. 2016). As most masting occurs when the previous year was cooler, this suggests more regular masting events, increasing seed production but also increasing the number of exotic mammalian seed predators (Choquenot & Ruscoe 2000, Kelly & Sork 2002). The response of different masting species is likely to be spatially variable and taxon-specific (Allen et al. 2014). The effects of climate change on mast seeding species are complex and while a large degree of uncertainty remains, it is one of the better-understood processes that may be influenced by a changing climate in New Zealand (Kelly et al. 2013).

The increasing variability of weather as well as increasing temperatures may assist in increasing the amount of successful sub-tropical invasive plants who are now able to overcome an environmental threshold (Sheppard et al. 2016). This would likely have impacts on the native seed bank and ability of native trees to germinate in areas with more vigorous non-native flora. For example, Giejsztowt et al. (2020) under the warmer temperatures created by climate change, found a four-fold increase in native species and non-native weeds flowering at the same time, leading to reduced seed mass for high-density floral patches. The evidence suggests that the presence non-native flowers increased the competition for pollination services to the point where native species were reduced in their reproduction capability (Giejsztowt et al. 2020).

Table 4: Summary of New Zealand specific studies exploring impacts of climate change on woody species (Lundquist et al. 2011, Keegan et al. 2022)

Climate Change Process	Ecosystem or Species Impacted	Type of Evidence	Mechanism and Impact	References
Warming Temperatures	Alpine Flora	Field experiment	Changed phenology of native plants, increasing competition for pollinator services. Potential disruption of pollination.	Giejsztowt et al. (2020)
Warming Temperatures	Southern beech species, Mountain beech	Field study and modelling	More frequent seed production at higher elevations.	Letherwick & Austin 2001, Richardson et al. (2005a),
Warming Temperatures and rainfall shifts	Kūmarahou (<i>Pomaderris kumeraho</i>)	Modelling	Changing climate shifts the likely distribution of culturally important species, likely reducing access.	Bond et al. (2019)
Drought	Kauri (<i>Agathis australis</i>)	Field Study	Natural drought increased leaf litter fall in kauri. Kauri litter reduces germination of non-kauri.	Macinnis-Ng & Schwendenmann (2015)
Warming Alpine zone	Vulnerable alpine biota	Field observations and Modelling	Decline in vascular plant and invertebrate taxa. Decline of potential pollinators.	White & Sedcole (1991), Halloy and Mark (2003), Winterbourn et al. (2008), Chinn & Chinn (2020)
Range of factors including: warming temperatures, less rainfall, increased fire regime	Invasive flora	Modelling and field studies	Establishment and spread of invasive species favoured by changes. Change of seed rain/seed bank potentially increasing resource competition for native species.	Field & Forde (1990), Perry et al. (2014), Sheppard & Stanley (2014), Sheppard et al. (2014, 2016), Thuiller et al. (2007)

3.2 Fire, Flood, Landslides, and Wind

Fire is a driving ecology force in many ecosystems, though in pre-settlement New Zealand there was limited influence, with schedules estimated to be centuries if not millennia for same-site fires (Wilmshurst et al. 1997, 1999, Rogers et al. 2007). Humans have changed Aotearoa's fire regime both temporally and spatially with fire occurring more frequently as well as impacting more fragmented landscapes (Perry et al. 2014). According to modelling in Perry et al. (2015), removal of seed predators thus allowing forest succession to proceed to a state of less flammable mature vegetation could assist in fire control in the future. Generally speaking, this removal of seed predators and resulting less frequent fire would both contribute to increases in natural germination. The majority of study on fire in the New Zealand ecosystem has been done on negatively impacted species, here we will attempt to comment on positively impacted woody species and germination in particular.

The primary impact of fire is vegetation death, which has a rather obvious impact on ability to produce seed. In general, New Zealand native tree species are known to have relatively thin bark, which makes them more vulnerable to death by fire, meaning that an increasing fire regime is likely to reduce the amount of seed available from fire affected populations (Perry et al. 2014). Woody species in New Zealand have few specific fire adaptations with those that do (*Leptospermum scoparium*, *Kunzea sp.*, *Discaria toumatou*) being related to Australian species, which would have higher exposure to fire on the evolutionary timescale (e.g. de Lange et al. 2010). New Zealand species do have some resprouting capability after fire, but *Leptospermum scoparium* is the only New Zealand native tree species that demonstrates massive seed release after fire (Perry et al 2014), taking advantage of the germination

sites that develop post fire. Yet, there is also no evidence that high heat increases mānuka germination (Battersby et al. 2017). Germination stimulation by smoke compounds has not been identified in New Zealand species, though testing has been done on restiad bog species as well as mānuka (Battersby et al. 2017, Wilson et al. 2022). See Table 4 below which shows the list of New Zealand fire adapted woody species that would present lasting seed sources even when facing higher wildfire risk.

Table 5: Woody species in NZ which are adapted or tolerant of fire (Burrows 1994a, Perry et al. 2014, Wabnig 2014).

Species	Life-form	Seed release post-fire	Resprouts
Fire Adapted Species			
<i>Cordyline</i> sp. (e.g. tī kōuka)	Monocot Tree	N	Y
matagouri (<i>Discaria toumatou</i>)	Shrub	N	Y
kānuka (<i>Kunzea</i> sp.)	Tree	N	N
mānuka (<i>Leptospermum scoparium</i>)	Small tree	Y	N
Fire Tolerant Species			
makomako (<i>Aristotelia serrata</i>)	Tree	N	Y
putaputawētā (<i>Carpodetus serratus</i>)	Small tree	N	Y
<i>Dracophyllum</i> sp.	Shrub-Tree	N	N
kōtukutuku (<i>Fuchsia excorticata</i>)	Tree	N	Y
kāpuka (<i>Griselinia littoralis</i>)	Shrub	N	Y
māhoe (<i>Melicytus ramiflorus</i>)	Tree	N	Y
tauhinu (<i>Ozothamnus leptophylla</i>)	Shrub	N	Y
<i>Pittosporum</i> sp. (e.g. kōhūhū)	Tree	N	Y
tōtara (<i>Podocarpus totara</i>)	Tree	N	Y
<i>Pseudopanax</i> sp. (e.g. horoeka)	Tree	N	Y
kāmahi (<i>Pterophylla racemosa</i>)	Tree	N	Y

Floods are another episodic ecosystem event which opens the canopy structure of a forest and allows for new individual recruitment. Westland New Zealand has shown a history of flood events as maintaining podocarp succession, though little is known outside of this region (Duncan 1993). However, flooding in Turakina Valley in 2004 does provide some additional insight into the germination of tawa, rimu, māhoe, with seedlings able to germinate in the newly deposited flood sediments, though tawa and rimu were unable to persist due to competition with non-native herbaceous plants (Redpath & Rapson 2015). This emphasises the ability to germinate on fresh mineral soils, but confirms that tawa seedlings rarely persist outside of protected, highly shaded locations (Knowles & Beveridge 1982, Lusk 1984, Lusk et al. 2009, Redpath & Rapson 2015).

Landslides as erosion events create challenges for germination. New Zealand is a relatively dynamic landscape given its position across the Australian-Pacific tectonic boundary, with uplift movement up to 10mm per year across the Southern Alps contributing to landscape instability (Bellingham & Lee 2006). Species limited by

dispersal will have difficulty competing for available germination sites. Also, the loss of topsoil will contribute to reduced nutrient availability for seedling recruitment. Hewitt (1996) was able to quantitatively measure approximate topsoil loss over 40 years in dry environments. Loss of topsoil depth was patchy, and was greatest (8.5 mm per decade) on ridge crests and north-facing upper slopes with south-facing aspects and lower parts of north-facing slopes usually having a net increase (0.08 and 0.16 mm per decade, respectively). These relative losses and gains suggest that wind erosion rearranges soil on a local scale, and that soil loss is restricted to upper parts of ridge crests (Hewitt 1996). This has implications for afforestation as most revegetation projects occur on sloped land where there will be increased nutrient loss that would negatively affect the ability for natural germination and recruitment to be successful given the lowered nutrients available. Also, if a site is physically unstable, this would prevent slower germinating species from becoming established before being buried or otherwise disturbed. Bellingham et al. (2001) found that scented broom (*Carmichaelia odorata*) increased nitrogen levels in the soil, facilitating the germination of three other successional species (kāpuka, southern rātā, and kāmahī) at varying responsive rates. Low soil nitrogen and phosphorus were found to be limiting factors for slip colonisation in other parts of the world (e.g. Walker et al. 1996, Walker et al. 2009). This suggests that loss of nutrient dense topsoil from erosion events has an effect on germination ability, though outside of nutrient availability this has not been studied for New Zealand woody species. Grazing by feral and domestic mammals is also known to increase erosion rates and thus would exacerbate any effects on germination (Bellingham & Lee 2006).

Given the long, thin nature of New Zealand as well as central mountain ranges, winds can be extreme especially along the eastern sides of the island and in the hill country (Wardle & Platt 2011). Some estimate that wind is a major ecological influence in pre-human forests, much like fire is a feature in Australian forests (Wardle & Platt 2011). Wind damage in a forest is known to affect germination and succession as the damage created tends to be relatively low in mortality and relatively high in the creation of leaf litter (Everham & Brokaw 1996). This may lead to reduced germination of pioneer species that require open ground and high light situations for recruitment success, though the upturning of root balls may provide some microsites that are suitable (Schaetzl et al. 1989). Storm damage in the early 20th century in New Zealand was thought to cause recruitment of tawa and southern beech species given the somewhat low disturbance of low-growing vegetation and soil layers (Martin & Ogden 2006). The global southern limit of trees (which is the Nothofagaceae family) has been attributed to wind, rather than temperature, affecting recruitment and growth (Buma et al. 2020). Winds of the polar vortex are increasing at approximately 1% per year due to the large-scale warming and stratospheric ozone depletion association with climate change (Young et al. 2011, Thompson et al. 2011, Zhang 2014). This suggests that though warmer temperatures can cause shifts in treelines, increasing wind speeds may prevent germination and survival beyond the current observed tree limit for New Zealand's southernmost islands.

Abiotic Factors

This section will explore the physical factors which may impact germination in the New Zealand environment. Microhabitat variation can play a facilitative role by regulating the burden of stressful events associated with extreme temperatures, low soil moisture availability, periods of intense solar radiation or combinations of these factors (Körner 2014, Körner et al. 2016, Körner & Hiltbrunner 2017). Important microhabitat features include the effects of shade, soil conditions and chemistry, fungal pathogens, temperature, aspect, slope, water availability, timing, competition with conspecific parents, or with other vegetation (Grubb 1977). Discussion will include the impact of abiotic factors on tree's ability to produce seeds as well as acting as a continuing seed source despite hostile conditions.

3.3 Soil Nutrients

There is suggestion that New Zealand woody species are adapted to low fertility soils with previous studies showing that higher fertility sites are more rich in exotic species (Timmins & Williams 1991, Craine et al. 2006). Soil fertility varies across New Zealand temperate rainforests due to heavy rainfall causing erosion which leaches nutrients from ridges to downslope and gully areas (Richardson et al. 2008). Evidence does show that levels of nitrogen and phosphorus in particular can affect seedling recruitment, and thus seed germination (Clarkson et al.

2002, Walker et al. 2003). Carswell et al. (2007) explored the interaction of phosphorus and nitrogen with seedling survival, showing that high soil nitrogen assisted on all species regeneration, particularly mataī and kahikatea. Miro and rimu germination and seedling survival decreased with increasing soil phosphorus and did not affect tawa. In terms of natural regeneration, Podocarp colonise and grow in areas where the soil has high nitrogen levels, but low amounts of phosphorus (Carswell et al. 2007). Regardless of soil nitrogen quality kākūka and tauhinu germinated and survived well, suggesting that nitrogen content has no significant impact on their ability to germinate (Cieraad et al. 2015). Kōhūhū rates of growth increased linearly with soil nitrogen and all species were faster growing than invasive species in high nitrogen scenarios (Cieraad et al. 2015). When examining soil phosphorus gradient across coastal sand plains, there was no evidence of impact on plant establishment success (Zhong et al. 2021). In a study of soil fertility on functional plant traits, it was found that seed mass is positively correlated with soil fertility, though this was likely due to the dominance large-seed species (e.g. kohekohe, tawa, karaka) in the shady, more fertile areas of the study rather than any comment on plant fitness (Jager et al. 2014).

There is evidence from the study of crop species that certain ions of potassium (K), iron (Fe), zinc (Zn), and copper (Cu) assist with the mobilisation of proteins during seed development (Martínez-Ballesta et al. 2020). Sulphur (S) deficiency in barrel clover (*Medicago truncatula*) was shown to reduce seed mass and delay germination through reduced levels of sucrose and protein in the seed (Zuber et al. 2013). Unfortunately, this area is unstudied for the germination native New Zealand trees but may be especially relevant in the restoration of agricultural areas where soil nutrient profiles have been altered.

Overall, the specific effect of soil fertility and micronutrients on germination is sparse for a wide range of New Zealand native trees, though the idea of low fertility soils being preferred habitat has generally been dismissed despite adaptations to survive in lower nutrient soils.

3.4 Soil pH

The vast majority of research into soil pH has been focused on the improvement of legume growth in pasture to better support animal agriculture in New Zealand (Morton 2020). Native forest soils are known to be slightly more acidic than agricultural soils, which undergo further acidification when turned to pasture and grazed by livestock (During 1984, Kim et al. 2015). This has led to the widespread use of lime to neutralise soil pH to improve pasture quality (Morton 2020). When soil pH is below 5.0, it has been shown to reduce rhizobia nodulation for legumes, and also reduce earthworm activity (During 1984, Kim et al. 2015). Relevant to plant germination and survival is the immobilisation of phosphorus in soil with low pH, which may also create further negative impacts on the solubility of nutrients and toxic metals (Kent 1982, Wong 2003, Todd et al. 2009).

Kauri trees through leaf litter deposition reduce germination of other native species through decreased soil pH, which reduces overall soil fertility (Jongkind et al. 2007, Wyse & Burns 2013). There was a marginal decrease in kōtukutuku biomass, but not germination due to lower soil pH as caused by ungulate presence (Kardol et al. 2014). When exploring revegetation of coal mining waste rock, it was supposed that low pH reduced recruitment and survival of kōhūhū and mānuka, though they have some natural tolerance for acidic environments (Todd et al. 2009).

Overall, the effects of overly acidic soils on indigenous tree species is not well understood. For plants in general, nutrient availability is maximised at a pH of approximately 6.5 (Harris et al. 1996).

3.5 Moisture

Water is a primary germination regulator (Baskin & Baskin 2003). Moisture is required for seeds to germinate as water penetration (seed imbibition) is an essential trigger for embryonic development. This can be seen clearly in seeds with physical dormancy that require treatments to soften the seed coat to allow water passage into the embryonic tissues. It is necessary for enzymatic reactions and the mobilisation of the seed storage reserves, including lipids, carbohydrates, and proteins (Szczerba et al. 2021, Sghaier et al. 2022). A water shortage inhibits the enzymes responsible for hydrolysing endosperm starch, which supplies energy for plant development by metabolising sugar (Muscolo et al. 2014).

The majority of pollen and seeds undergo a decrease in water quantity prior to dispersal. The remaining water amount is variable (between 2 - 70%) which leads to variable response of seeds to relative humidity for

viability over time and for germination (Franchi et al. 2011). Seeds that do not dry as part of maturing are shed at 30-70% moisture content and are termed recalcitrant, meaning they are likely unable to be stored for long periods of time (Franchi et al. 2011). Low moisture soils have been shown to cause increased amounts of exotic vegetation on the South Island (Cieraad et al. 2015). This suggests that New Zealand native species are less competitive in dry environments.

There have been significant studies into germination by Burrows throughout the 1990s, and these clearly show the importance of water availability for seed germination.

3.6 Temperature

While temperature does have a large effect on the timing and rate of germination, there has been little published on temperatures specific to New Zealand woody species outside of “standard” germination practices (Burrows 1993-1999). Many germination protocol tests have been done with standard temperatures being approximately between 20-24°C, which sits within reasonable glasshouse temperatures (Burrows et al. 1991, Fountain & Outred 1991, Rowarth et al. 2007). Low temperatures inhibit germination to avoid seedlings growth during winter conditions with a rise in temperature conditions, as is naturally encountered in soil in spring, known to stimulate a flush of germination across a wide range of species (Rowarth et al. 2007).

Specific temperatures are more commonly found in dormancy breaking protocols, where specific high temperatures are required for breaking PY or combinational dormancy. This was discussed in the previous section discussing dormancy alleviation for akeake, kōwhai, and kakabeak.

3.7 Light and Shade

Light has been shown to improve the germination of a wide variety of New Zealand woody species (Bannister & Jameson 1991, Fountain & Outred 1991, Rowarth et al. 2007). Formation of canopy gaps are considered an important driver of forest succession (Whitmore 1989). It has been found in New Zealand that the creation of favourably light conditions in canopy gaps supports both increased richness in species germination and establishment, with species richness thought to be limited by availability of seed and/or seed dispersal (Tulod & Norton 2020).

Beech seedlings have proven to be particularly vulnerable to sudden increases in their light environment (Tognetti et al. 1998, Reynolds & Frochot 2003). Young mountain beech germinants show impressive adaptation to the high light conditions in growing in subalpine environments (Döweler et al. 2021). This challenges previous findings of photoinhibition, instead proposing that a lack of frost tolerance in summer as the controlling factor in treeline formation of mountain beech (Döweler et al. 2021). This holds true for a variety of higher altitude woody species, but many tall native tree species which have significantly higher germination under shady conditions (Young 2012). A study by Lusk et al. (2009) showed that rimu and miro were able to establish across all light levels, similar to tawa and māhoe. Overall, rimu and tawa were the most shade tolerant as seedlings, with miro, māhoe, and *Ixerba brexioides* (tāwari) most likely to occupy mid-light availability microsite locations. Kāmahi and hīnau required brighter minimum levels and were underrepresented in deep shade. (Lusk et al. 2009)

In a field experiment with pohutukawa, germination was reduced with increasing open sky while kōtukutuku germination was increased in canopy gaps with higher light availability (McAlpine & Drake 2003).

Shady microsites likely have higher moisture and are more protected from desiccation cycles compared to more open sites (Sessions & Kelly 2000, Young 2012). Also, sunny sites tend to be dominated by exotic grass species which form thick swards with low canopies which create significantly different microsites when compared to native tussock grasses (Ingraham & Mark 2000, Sessions & Kelly 2000). This shady factor was a major contributing factor for the regeneration of native species below exotic canopies, where shade intolerance appears to be the dominant restrictive factor for non-native regeneration (further discussed in the biotic factor section below).

3.8 Microsite

Successful germination microsites (scaled from 0.01 - 1000 m) are multi-dimensional and often transient, with conditions changing often given environmental and weather instability (Oke 2002, Hampton et al. 2005). The five variables which characterise this scale are: sunlight, moisture content (air and soil), precipitation, wind

exposure, and temperature (Davies-Colley et al. 2000). In comparing the microsite conditions in native forest to pasture, the forest floor was much less windy (approximately 20% less), shadier (0.76% of open area light exposure), and fluctuates much less in both moisture and temperature (Davies-Colley et al 2000). At the forest edge, light and soil temperature showed the largest gradient when compared to air temperature and wind speed, with edge effects reaching approximately 40m beyond the forest edge itself (Davies-Colley et al. 2000). Young & Mitchell (1994) suggested that forest fragments less than 9ha are fully possessed by edge effect with forest under 1ha missing interior forest conditions completely. These micro-environmental gradients have been shown to affect the germination and regeneration of black beech in mānuka scrub with canopy edge position showing the highest emergence (24.6-30% at edge, 6.4-9.2 under dense canopy, and 0.6-4.4% in the open), highlighting the benefits of partial shade and resulting higher moisture balance as beneficial for seed germination (Davis et al. 2013)

Trees that produce small seeds are commonly observed to be microsite limited, meaning more seed existing in the environment than sites for germination which can be utilised (Crawley 1989, Dalling & Hubbell 2002, Zeiter et al. 2006). This is opposed to seed limited species, which tend to produce larger seeds, for which many more suitable microsites exist than viable seed (Eriksson & Ehrlén 1992, Coomes & Grubb 2003, Berry 2006). Examples of small-seeded native tree species include: pōhutukawa, rewarewa, kāmahī, and rātā. Examples of large-seed native tree species include: tawa, taraire, kohekohe, and karaka. Seedling establishment is further limited by the availability of suitable microsites, particularly in the alluvial forests, where the dense canopy and ferns create deep shade (Coomes et al. 2005). Silver beech seedlings were more likely to establish on elevated surfaces than on the forest floor of both forest types (Coomes et al. 2005).

Seed germination is generally advantaged by burial due to increased moisture availability and reduced consumption via predators (e.g. Chauhan et al. 2006, Orrock & Damschen 2007), though higher depths can reduce emergence (e.g. Oldham & Ransom 2009, Zhu et al. 2009). This benefit is not realised by introduced rodents in New Zealand as none of them are larder or scatter hoarding rat species, but sometimes carrying food elsewhere before consuming (Vander Wall 1990). In a study looking at seed burial by seabirds in New Zealand, germination of native species from soil samples in bird-occupied spaces showed significant increase in germination from shallow soil layers (0-59 mm) in comparison to germination in deeper soil samples (Grant-Hoffman et al. 2010).

Presence of woody debris can also create valuable microsites for germination by increasing structural heterogeneity and nutrient cycling, which can have ramification for fungal mutualism functioning especially (Allen et al. 2003, Richardson et al. 2009, Allen et al. 2016). Deadwood also alleviates the most intense shade through exclusion of understory plants, prevents seed predation and herbivory of young seedlings, and reduces root competition (Richardson et al. 2009). Though there is no information specific to effects on following germination, the death of canopy trees and the decay of the coarse woody debris that they generate on the forest floor results in altered concentrations of soil calcium (Allen et al. 1997), nitrogen (Zimmerman et al. 1995), and altered pools of carbon (Fahey et al. 2005).

3.9 Heavy Metals and Mining After Effects

Mechanistically, the toxic effects of metals on plants include the inactivation of enzymes, impairment of membrane function and loss of membrane integrity, deranged nutrient absorption, cell damage, or precipitate or chelate formation with essential plant metabolites. The threat by heavy metals to plants and consequently to humans and other animals is further provoked by poor movement and their ability to persist in the environment (Zaidi et al. 2012). Plant germination on mining waste in particular is thought to be limited by reduced levels of topsoil, being inhibited by the crushed rock substrate (Wong 2003). Heavy metals, like cadmium, are known to have negative effects on germination, and while the specific germination processes affected are generally unconfirmed, their negative correlation with water uptake and water movement is likely to impact germination and lower water stress tolerance (Barceló et al 1986, Poschenrieder et al. 1989). Some grasses seem to be tolerant of heavy metals and present an opportunity for mine waste rock reclamation and preparation for subsequent woody species (Morrell 1997).

In New Zealand, dense vegetation was able to establish on siltstone dominated waste rock. Quartz pebbles as waste rocks were less favourable due to low moisture capacity, high mobility/erosion prone nature of the surface causing loss of seeds with rainfall. Quartz pebbles substrate of more than 35% led to sparse plant cover, quartz

pebble substrate between 15-30% led to scattered plant cover and quartz pebbles substrate between 5-15% cover led to full vegetation and soil formation. (Todd et al. 2009). Gregg et al. (2000) determined that three indigenous species (kānuka, tī kōuka, kōhūhū) could be planted directly into mining tailings if required at the Waihi gold mine in the north-east of the North Island.

Biotic Factors

This section delves into the multifaceted interaction of biotic factors that play pivotal roles in influencing tree seed quality and germination. Management decisions around pest and weed control, biosecurity concerns, and utilisation of existing positive feedback loops are important considerations when investigating pathways to increase native forest regeneration. These interactions can also influence the capacity of the forest to supply seed to the growing native forestry industry. The interplay of seed and the living organisms in their environments are discussed below.

3.10 Mycorrhiza

Mycorrhizal fungi are a class of fungi which form mutually beneficial symbiotic relationships with living plant roots (Thomas & Spurway 1997, Aislabie & Dymond 2013). Ostensibly, all seeds which germinate in soil do so within a wide fungal network which is pre-existing in that growing medium, also contributing to physical structure of soil (Thomas & Spurway 1997, Harris 2009). While impacts of mycorrhizal relationships on germination is typically not the focus of study, the fungal communities which exist in soil have major impacts on the successful establishment of seedlings. In low fertility soils, these fungal associations allow for greater nutrient uptake (Thomas & Spurway 1997). AMF accesses inorganic rather than organic nutrient sources which leads to their hyphae proliferating within mineral soil; conversely ECM accesses more organic nutrient sources thus existing more within the litter layer (Smith & Read 2008, Williams 2010). Mineral soil therefore contains more AM material while leaf litter contains more ECM, which is important when considering collection of mycorrhizal inoculant for use within nursery seedling production for species which are obligate ECM mutualists.

Mycorrhiza are hugely important to the acquisition of nutrients for a large majority of the globe's plant life, play significant roles in the cycling of major nutrients, and are considered fundamental drivers of ecosystem functioning and adaptation (Smith & Read 1997, Simard et al. 2012, Aislabie & Dymond 2013). The partnerships formed can be obligate for trees either with arbuscular or ectomycorrhizal mutualisms developing, and inoculation of seeds or seedlings often mediate species' invasions into previously unoccupied areas (Dickie et al. 2012, Davis et al. 2013b, Rundel et al. 2014). In New Zealand, only three native woody plant groups (kānuka, mānuka, and the southern beeches) are known to host ECM, forming symbioses with approximately 76 fungal genera (Orlovich & Cairney 2004). Outside of ECM relationships, both podocarps and angiosperm seedlings growing in the field have been observed having high levels of AMF colonisation (Hurst et al. 2002).

In native New Zealand woody species, these mutualisms are most studied in the southern beech species and scrub species as there is an interesting phenomena of limited spread of beech trees into grassland and various "Beech gaps" are known to exist, previously without explanation (Wardle 1984, Wiser et al. 2011, Rundel et al. 2014, Barber-Sperling 2023). Mānuka and kānuka have been confirmed as hosts for both ectomycorrhizal and arbuscular mycorrhizal species, acting as soil community facilitators for later invasion of obligate ectomycorrhizal partners (Dickie et al. 2012, Simard et al. 2012). AMF have no saprotrophic capacity, meaning they depend on bacteria and other decay fungi to acquire nitrogen to pass on to their plant partners (Leigh et al. 2009, Hodge & Fitter 2010). This is further linked to ECM dominated plant communities having relatively lower species richness with ECM being observed to affect mineralisation of soil nutrients, making fewer nutrients available for AMF partnered plants (Dickie et al. 2014).

Overall, there is very little information on how mycorrhizal inoculation affects germination rather than overall recruitment for New Zealand woody, but findings and potential interactions are summarised below:

Kānuka establishment in exotic grassland has been shown to be constrained by lack of mycorrhiza amount in the soil community. This necessary abundance in the fungal community was disproven as a restriction for mānuka

establishment of grassland (Davis et al. 2013a). Under mountain beech, the soil is dominated by ectomycorrhizal colonisation. This prevents obligate AMF mutualistic plants from establishing at particular microsites, with more diverse understories present in areas with AMF (Spence et al. 2011). Though two studies found ectomycorrhizal infection in all *Lophozonia menziesii* (silver beech) larger than 10cm despite distance from host trees (Allen 1987, Rogers 1989), lack of inoculum is likely to not be a complete barrier, but a filter against weaker seedlings (Dickie et al. 2012).

Table 6: List of references to find specific fungal-plant host associations of New Zealand native trees.

Species	Reference
Mānuka, Kānuka, Southern Beech	Orlovich & Cairney 2004
Mānuka, Kānuka	Moyersoen & Beever 2004, McKenzie et al. 2006, Weijtmans et al. 2007, Wicaksono et al. 2018
Mountain Beech	Spence et al. 2011
Kauri	Padamsee et al. 2016
Mountain Tōtara	Williams et al. 2012
Ramarama	Ford et al. 2018
Miro, Mataī, Rimu, Kahikatea	Russell et al. 2002

The class of hormones known as strigolactones, has recently been identified that functions as signalling compounds in symbiosis, particularly for preparation for penetration by AMF hyphae. There is potential overlap in early forming (at seed stage) mycorrhizal mutualisms or location of seed near colonised roots to also trigger germination via impacting the production of strigolactones (Parniske 2008). Fungal exudates facilitate early root morphology in AMF colonisation. High AMF colonisation and subsequent higher phosphorus acquisition generally increase auxin and cytokinin and decrease ethylene and strigolactone levels. While direct impact on germination is not explored, the potential impact of fungal exudates on endogenous plant hormones suggests a potential pathway of interaction (Fusconi 2014).

3.11 Bacteria, Viruses, Parasites, and Disease

The study of bacteria for germination interactions is a new global area of study mainly focused on crop species. Pink Pigmented Facultative Methylophilic Bacteria (PPFMs) are common if not universal bacterial symbionts which are affiliated with the seeds, roots, and leaves of terrestrial plants, but can also be free living. Though no New Zealand specific examples exist, they are known to positively affect germination of sugarcane and several Californian native plants (Madhaiyan et al. 2005, Irvine et al. 2013). PPFMS affect plants via secretion of hormones (including auxins, which have been shown to impact germination processes), ureases, alcohols, and sugars (Irvine et al. 2013). In the first study of PPFMs in New Zealand showed eleven different species found to be in association with native plants of New Zealand, the highest number of associations in trees being methylobacterium found in kawakawa, mānatu, tītoki, and kōhūhū. Fewer associations were found in an additional seven native tree species, but this may have been a reflection of the poor interaction between leaf structure and experimental protocol (Jahan 2013). In a first exploratory study on a New Zealand native plant, Endophytic actinobacteria was found on horopito, and significantly affected plant growth though germination itself was not tested (Purushotham et al. 2018). This type of bacteria has been shown to increase plant growth, protect from biotic and abiotic stressors, and increase resistance to phytopathogens. The promotion of plant growth by actinobacteria is similar to other germinant supporting mechanisms as seen in increasing nutrient availability and secreting phytohormones (Purushotham et al.

2018). Further exploration may lead to future understanding of the effects of the microbiome of native trees and how germination may or may not be affected.

Viruses as lifeforms are the most simple obligate parasites, with approximately 220 plant viruses invading NZ in the last 200 years with numbers still increasing (Veerakone et al. 2015). While germination effects have not been studied in particular for native tree infections, virus infections can be passed vertically through seed, contact, and aphids, and are known to affect growth and health of plants (Guy et al. 2022, Veerakone et al. 2015). As native seedling production expands, prevention of viral spread through operational protocols in nursery systems will likely be important to avoid potential germination failures and production of healthy seedlings for planting projects (Guy et al. 2022). Control of these will be especially relevant in nurseries which also produce exotic seedlings, which are the major host group of these viral diseases.

Table 7: List of Viral, Viroids, Phytoplasmas, Bacteria disease found in NZ native woody species, often hosted by widely utilised crop species.

Native Host	Disease Agent	Reference
Poroporo - <i>Solanum laciniatum</i>	<i>Alfalfa/Lucerne Mosaic Virus, Cucumber Mosaic Virus, Potato Virus X, Potato Virus Y, Tobacco Mosaic Virus, Tomato Spotted Wilt Virus, 'Candidatus Liberibacter solanacearum'</i>	Fletcher (1983), Baylis (1966), Thomson (1976, 1979), Labas et al. (2006), Vereijssen & Scott (2013)
Kawakawa - <i>-piper excelsum subsp. excelsum</i>	<i>Cucumber Mosaic Virus, Tobacco Ringspot Virus</i>	Labas et al. (2006)
Kōwhai - <i>Sophora microphylla</i>	<i>Tobacco Ringspot Virus</i>	Ward et al. (2009)
Akapuka - <i>Griselinia lucida</i>	<i>Tomato Ringspot Virus</i>	Veerakone et al. (2010)
Karaka - <i>Corynocarpus laevigatus</i>	<i>Cucumber Mosaic Virus</i>	Ashby (1977)
Large-seeded coprosma - <i>Coprosma macrocarpa</i>	<i>'Candidatus Phytoplasma australiense' - Coprosma Lethal Decline</i>	Beever et al. (2004)
Karamū - <i>Coprosma robusta</i>	<i>'Candidatus Phytoplasma australiense' - Coprosma Lethal Decline</i>	Beever (2001), Beever et al. (2004), Beever et al. (2008), Winks et al. (2014)
Tī kōuka - <i>Cordyline australis</i>	<i>'Candidatus Phytoplasma australiense' - Cordyline Sudden Decline</i>	Rees-George et al. (1990), Beever et al. (1996), Andersen et al. (2001), Beever et al. (2008), Winks et al. (2014)
Tī ngahere - <i>Cordyline banksii</i>	<i>'Candidatus Phytoplasma australiense' - Cordyline Sudden Decline</i>	Andersen et al. (2006)
Poroporo - <i>Solanum aviculare</i>	<i>'Candidatus Liberibacter solanacearum'</i>	Vereijssen & Scott (2013)

3.12 Myrtle Rust

The pandemic biotype of Myrtle rust (*Austropuccinia psidii*) arrived in New Zealand in 2017, thought to arrive by spores carried on strong winds from eastern Australia (Stewart et al. 2018). It infects the growing shoots of plants as well as the fruiting bodies in some species (Hood 2016, Beresford et al. 2019). New Zealand has 27 native myrtle species, with the most susceptible species being pōhutukawa, ramarama (*Lophomyrtus bullata*), rōhutu (*Lophomyrtus obcordata*), though some resistant seedlings were identified in mānuka, and *kunzea* species. In serious infections, it is possible for this rust to destroy growing parts of highly susceptible plants as has been observed in the collapse of mature trees and leading to significant changes in eastern Australian forests (Carnegie et al. 2016, Pegg et al. 2017). In the field, *Lophomyrtus* species developing fruits are infected causing the premature seed to drop (Beresford et al. 2019). The repeated infection of these species leading to death of seed-bearing mature trees means that local extinction is now considered probable, especially as the most active season for myrtle rust infection overlaps with the fruiting and seeding period of *Lophomyrtus* species (Beresford et al. 2018, Beresford et al. 2019). Luckily, the rare swamp maire and rātā mochau have not shown any evidence of being affected (Beresford et al. 2019).

Worldwide, young seedlings in nurseries with their high amount of young, growing shoots have been most affected, with nurseries in New Zealand now facing increased rust control procedures and sometimes choosing to avoid production of myrtle species entirely to avoid risk (Tommerup et al. 2003, Makinson 2019, Beresford et al. 2019). Impacts on germination are thus confirmed in both reduced seed availability for *Lophomyrtus* in the wild, and in the logistical constraints in nursery production. These issues are likely to be further exacerbated by decisions made around species choice for restoration projects in the warmer regions excluding myrtle species as has been decided by Auckland Council in 2019.

3.13 Kauri Dieback

Kauri Dieback (*Phytophthora agathidicida*) was initially reported in 1974 on Great Barrier Island in 1974, though it is thought that it was initially established in a Waipoua nursery then spread to other sites by New Zealand Forest Service planting activity in the 1950s (Black & Dickie 2016). Lethality studies have been limited to young seedlings in controlled conditions for obvious reasons. When the pathogen is injected directly into the stem, 100% of seedlings perish within 4-6 weeks, and when soil is inoculated, 100% of seedlings are killed within 10-12 weeks (Horner & Hough 2014). Kauri are positioned as foundation species in northern New Zealand, influencing the soil environment, hydrology, and ultimately the unique mix of tree species able to associate with them as the forest community (Wyse et al. 2014, Macinnis-Ng & Schwendenmann 2015). The thick litter created by Kauri, who contribute approximately 80% of litter, creates highly acidic conditions, reduces nitrogen availability, and can also lead to anaerobic conditions within the soil (Wyse et al. 2014). These drastic effects on soil conditions have major impacts on the germination of, and the eventual make up of kauri forest with a distinct mix of hardwoods, conifers and podocarps (Wyse et al. 2014). Alongside the loss of kauri themselves, there are worries that the long-term changes to soil structure, soil chemistry, and soil microbial community will have permanent negative effects on the existence of kauri forest ecology into the future (Black & Dickie 2016).

3.14 Note on Germinating from Collected Soil Samples

Samples of forest floor are sometimes used as a method for small-scale nursery seedling production, particularly for species known to be difficult to germinate (e.g. genus *Elaeocarpus*). Presence of mycorrhiza, leaf litter, and chemical characteristics found in the soil have known effects on germination and establishment, as previously discussed for tawa. Native New Zealand species tend to persist for less time in the seed bank, preventing natural regeneration in the long term (Overdyck & Clarkson 2012). Germination from these samples takes place in a ‘natural’ soil microbiome, likely improving germination of some species due to maintenance of soil mutualisms. This practice may be helpful in identifying germination requirements if used in comparison to controlled germination practices.

3.15 Invasive Plant Species and Germination

Exotic species are known to create certain environmental conditions which can either facilitate or inhibit the germination and further survival of native woody species in terms of succession, with successful succession requiring successful germination. Williams (2011) describes 36 major exotic woody species that form lasting stands in New Zealand. 14 are described as being replaced by native species in some circumstances (*Buddleja davidii*, *Calluna vulgaris*, *Cytisus scoparius*, *Erica lusitanica*, *Hakea gibbosa*, *H. salicifolia*, *H. sericea*, *Leycesteria formosa*, *Lupinus arboreus*, *Racosperma longifolia*, *R. mearnsii*, *Rosa rubiginosa*, *Sambucus nigra*, and *Ulex europaeus*). A further 8 species are reported to have native seedlings beneath though replacement is uncertain (*Acer pseudoplatanus*, *Berberis darwinii*, *B. glaucocarpa*, *Chrysanthemoides monolifera* spp. *monilifera*, *Crataegus monogyna*, *Lycium ferocissimum*, *Salix cinerea*, and *S. fragilis*). The remaining 14 species have no records of replacement by native woody species or of having native species exist in their understory, though the lack of data around these species likely prevents the accurate assessment of some (*Lantana camara*, *Teline monspessulana*, (*Cotoneaster* spp., *Elaeagnus x reflexus*, *Ligustrum lucidum*, *L. sinense*, *Paraserianthus lophantha*, *Prunus* spp., *Pyracantha angustifolia*, *Racosperma dealbata*, *Rhamnus alaternus*, *Rhododendron ponticum*, *Solanum mauritianum*, and *Sorbus aucuparia*). In general, the shade tolerance of New Zealand seeds and seedlings appears to be a major factor in determining replacement of non-native woody species by native trees.

Non-native woody species have been observed to influence the composition of successional plant communities over time (Wotton & McAlpine 2013). Various biotic and abiotic factors contribute to successional outcomes, but a potential link exists between germination capability and the microsites created by these non-native species. Although the germination process under these non-native species remains understudied, comparisons between non-native and native species have been undertaken in specific instances, providing a general understanding of the species that native woody plants can successfully colonise. Exploring the factors in environments dominated by exotic species presents an opportunity to identify specific elements influencing germination. The relevant references and conclusion are summarised below.

Gorse (*Ulex europaeus*) is a widespread, nitrogen fixing woody weed species in New Zealand, known to be difficult to chemically control as well as having an extremely long-lived seed bank. Compared to māhoe, putaputawētā, karamū, kāpuka and tarata, gorse had significantly higher growth rates at 70% light exposure, but much lower growth rates at 11% light, while these light differences had no significant effects for the native species growth rates (Ogle-Mannering 1995). Overall, gorse does not regenerate well itself due to light intolerance of the seed and seedlings and succession by natives is expected in 50-60 years in situations without disturbance (Lee et al. 1986). In a comparison by Sullivan et al. (2007) of gorse versus kānuka, models repeatedly identified that presence of gorse and the following differences in vegetation were the significant impactors on creating differing species assemblages. Kānuka supported small-leaved species and increased abundance of kāmahi in particular. The identified differences between the kānuka and gorse stands were: dominance of naturalised bird species rather than native species, densely shaded short understory, greater leaf litter depth under gorse, increased soil nitrogen levels, increased moisture competition, fewer mycorrhizal associations (thus affecting soil phosphorus availability), and other differences in the soil microbiome. While it is suggested that gorse is a worse nurse crop for podocarps, this has not been experimentally proven. Māhoe was shown to do equally well under either species. (Sullivan et al. 2007).

Invasive brooms, including scotch broom (*Cytisus scoparius*) is another set invasive nitrogen-fixing species, dominating in colder and drier areas than gorse (Bascand & Jowett 1982, Department of Conservation Weeds database - Howell 2012). Two studies (Trass 2000, Burrows et al. 2015) confirm that addition of native seed under a living broom canopy led to increased species establishment for kāpuka, kōwhai and germination percentage, but not long-term survival of manatu. Seed addition did not increase abundance for kōhūhū or *Coprosma dumosa* (formerly *C. taylorii*) under broom. In both cases, the reduced light availability, slightly higher moisture, and light leaf litter amounts contributed to native seed germination and seedling survival while inhibiting broom regeneration.

Exotic conifers, *Pinus radiata* in particular, are an essential ingredient to the New Zealand forestry industry and yet are significant woody weeds across New Zealand. *Pinus cortata* (Lodgepole pine) and other conifers have become well established on more than 1.5 million hectares (New Zealand Wilding Conifer Management Group 2014). In some cases where harvesting of radiata pine has become non-viable economically, stands have been left to

age and provide an opportunity to study native woody regeneration underneath (Moles & Drake 1999, Casey et al. 2021). This system is also relevant for landowners who wish to transition from exotic pine forestry to permanent native forest including for the purpose of carbon storage (Forbes et al. 2019, Casey et al. 2021). In dryer conditions, radiata pine is likely to outcompete native woody species given the light condition under pine canopy (Ledgard 2008, Paul & Ledgard 2009). Thinning of the pine canopy, especially in more suitable moisture conditions, has been shown to speed the timeline of native woody regeneration (Ledgard 2008, Forbes et al. 2016). Radiata pine litter measuring at 3cm was found to improve the germination of kawakawa and tītiki, while not improving the germination of kōtukutuku (McAlpine & Drake 2003). In areas of the South Island where wilding conifers had achieved canopy closure, poisoning of the trees, as compared to felling and mulching, creating an excellent environment for native regeneration with no exotic species found underneath, the most common species being māhoe and shining karamū (*Coprosma lucida*) and the tallest found being kānuka and karamū (Paul & Ledgard 2009). Again, this success was attributed to the shade tolerance of native tree seeds and seedlings in comparison to exotics. This finding of native tree regeneration under poisoned conifer canopy was repeated again by McAlpine et al. (2016) under lodgepole pine with success attributed to lower competition. In a study comparing Douglas fir (*Pseudotsuga menziesii*), Lodgepole pine and mountain beech as both canopy dominant and recruited seedling showed that both non-native species had significant effects on the soil microbiome having: lower abundance and diversity of nematodes, lower soil organic matter, reduced microbial biomass, the mountain beech was also higher light availability and higher moisture content. These factors led to reduced native seedling survival under the two exotic species (Dehlin et al. 2008).

Under blackberry (*Rubus fruticosus*) there was germination and possible regeneration of kōhūhū, but not of *hoheria* sp. or of Hall's tōtara (*Podocarpus laetus*) (Wotton & McAlpine 2013).

In 2013, Wotton & McAlpine authored a decision-making document for which summarises the native forest regeneration capacity under non-native vegetation with the aim of refining resource utilisation for weed control. This document is recommended if a decision-tree style tool is needed for land management decisions across a wide variety of non-native woody canopy forming species. Under non-native species, the likelihood of native woody succession appears more pronounced, especially among those non-natives intolerant to shade. Various local factors, including moisture availability, leaf litter depth, disturbance frequency, and the presence of a native seed source, further influence the specific locational probability of native woody success. This underscores the significance of seed dispersal and the ability to germinate under low light conditions in determining the recruitment capacity of New Zealand native trees (Brockerhoff et al. 2003, Howell & McAlpine 2016). Post-germination, the presence of herbivorous animals becomes the ultimate determinant in the likelihood of native species supplanting weeds, with increasing herbivory strengthening the overall persistence of exotic weed dominance.

3.16 Non-Native Animal Impact on Germination

The introduction of mammals in particular has had significant impacts on the terrestrial ecology of New Zealand and overall composition of the forest (Nugent et al. 2001, Wardle et al. 2001). New Zealand has done the majority of global exclosure (enclosures excluding certain classes of animals) studies on plants, with approximately 80 paired sites across the country providing information on ungulate presence versus exclusion on a variety of site characteristics (Wardle et al. 2001, Spear & Chown 2009). Enhancements in germination speed and overall seed germination percentage post-gut passage do not always confer unequivocal benefits to the plant. The ultimate outcome, encompassing seedling survival and establishment, hinges on intricate interactions with various factors, including herbivory (Figuerola & Green 2004, Campos et al. 2008). Recent findings by Wotton & Kelly (2011) demonstrated that dispersal failure, stemming from seed predation by introduced mammals, significantly hindered the regeneration of New Zealand's two largest seeded tree species, affecting both seed germination and seedling survival.

It is noteworthy that factors crucial for seed germination may exhibit diminished relevance in subsequent stages of the plant cycle, such as seedling growth, establishment, and survival to adulthood (Harper et al. 1964). For example, a seed of a specific species may display enhanced germination under certain environmental conditions but could necessitate different conditions for successful establishment and progression to maturity. This would mean that while germination criteria are met, long term survival is not possible thus making the meeting of germination

criteria essentially irrelevant, especially where no genetic donation is made to future generations. Discussed below are the non-dispersal potential effects of non-native animals on germination of New Zealand native trees.

3.17 Deer and other Ungulates

It is well known that deer have significant effects on the composition and abundance of understory flora, usually facilitating invasions of non-native plants via inhibition of native plant survival, growth, and thus ability for seed production and resulting germination capacity (Relva et al. 2009). Population effects of red deer were modelled by Forsyth et al. (2015) for impact on forest composition over a 500-year timeline, with the largest repercussions predicted in high fertility forests when long term herbivory pressure on angiosperms led to dominance by conifer species. The feeding impacts and ecology of the extinct moa are significantly different from the current introduced ungulates in the New Zealand environment despite likely occupying much of the same habitat niche (Wood et al. 2008, Forsyth et al. 2010). While studies into germination are limited, the aforementioned network of long term paired exclosure sites provides a system for future comparison studies.

Deer tend to reduce foliage density and create a higher light availability in the understory (Veblen & Stewart 1982, Gill & Beardall 2001, Relva et al. 2009). As discussed in the previous section, more light availability tends to favour the recruitment of exotic plant species while higher shade situations allow woody natives to gain the upper hand. Evergreen species attract a lot of browsing through the winter, and the relatively large amount of evergreen native tree species will attract deer feeding. Overall reduction in foliage due to browsing reduces flowering and therefore seed production potential (Bellingham & Lee 2006). Deer can also affect seed rain and act as dispersers, though are not likely to be the main dispersal agents for New Zealand native trees, they are capable of instances of long-distance dispersal (Kelly et al. 2010). In the alpine context deer (*Cervus* sp.) had the highest amount of seed that was damaged or fragmented after gut passage compared to other animal seed dispersers with 10% fragmented, likely due to chewing (Wood et al. 2015).

Kāpuka, kōtukutuku, patē, kāmahī, *coprosma* sp. are preferred forages for deer and other ungulates, reducing these species and their ability to produce seed in ungulate occupied areas, while southern beech species are not preferred and horopito is avoided (Forsyth et al. 2010). Kāpuka is also eaten by fallow and sika deer (Golding 2000). Deer mostly feed in fertile areas and rest in non-fertile areas as shown at both Waitutu and on Stewart island, though the effect of this movement of soil nutrients, nor the impact of seeds being deposited on lower nutrient areas has not been studied in terms of germination percentages or rates (Forsyth et al. 2010). In general, though, we can infer that lower nutrient levels reduce plant performance overall, though specific rates of phosphorus affect podocarps in particular, with increasing nitrogen levels correlated positively with overall germination and seedling recruitment (Carswell et al. 2007)

Globally, herbivory has been shown to have both positive and negative effects on mycorrhizal association, but this has not been investigated in New Zealand (Gehring & Whitham 1994, Ashkannejhad & Horton 2006, Forsyth et al. 2010). Faecal pellets from European Red Deer (*Cervus elaphus*) and Australian brushtail possum resulted in ectomycorrhizal infection of pine with non-native mycorrhizal fungi, but faecal application did not result in the infection of the native silver beech with exotic or native fungal symbionts (Wood et al. 2015). This shows facilitation of invasion by exotic EM species through fungal infection via introduced mammal faeces and this benefit was not seen for native woody species (Wood et al. 2015). This was despite both exotic and native fungi known as being part of introduced mammal diets (Forsyth et al. 2002, Cochrane et al. 2003, Medway 2004). It seems likely that fungal associates with native woody species are evolved to insect or bird dispersal, showing that these introduced mammal species were unable to impart beneficial fungal infections to native woody species and further leading to soil microbiome changes that benefit non-native plant germination and recruitment (Wood et al. 2015).

Deer have greater foot impact than moa, but the impact of trampling by ungulates on germination has been studied. These trampling mechanisms are likely a major new effect on ground ecology in the New Zealand situation (Forsyth et al. 2010). There is some evidence that bulk density/microporosity and other soil abiotic qualities affect arbuscular mycorrhizal functioning (Kardol et al. 2014). Overall, deer show variable effects on soil abiotic factors which are known to affect germination, though exploration of germination processes in particular has not yet been studied.

Deer foraging on the most palatable species also produces leaf litter that is slower to decompose due to a higher concentration of foliar fibre in non-preferred species (Wardle et al. 2001, 2002, Forsyth et al. 2005). Quality of leaf litter (and thus potential impact on germination suitability as previously mentioned for impacting tawa) is context dependent for ungulates. In established forest with canopy coverage, changes to leaf litter qualities by ungulate herbivory are likely to be marginal given that larger trees are often not preferred and are long-lived species. Higher impacts on leaf litter are likely to be seen in disturbed, open-canopy or early successional situations with ungulates modifying leaf litter (higher nutrient content, lower structural carbohydrates and defence compounds) (Mason et al. 2010). The most notable effect of deer on soil was lower soil bulk density, which reduced plant growth for Karo (*Pittosporum crassifolium*). Soil bulk density was the only factor that was significantly affected across all measured enclosure sites (Mason et al. 2010). Lower soil organic matter, increased total carbon, and higher soil available phosphorus positively affected the growth rewarewa (Mason et al. 2010). Higher total carbon, and marginally lower total nitrogen and available soil phosphorus negatively affected the growth of karamū (*Coprosma robusta*) (Mason et al. 2010). These variable responses of soil abiotic factors to ungulate presence suggest impact on the competitive balance of co-occurring species, though there is no dominant factor in creating this change in competition (as was similarly found in Wardle et al. 2001). Thus, there are potential impacts on germination processes through changed leaf litter content (as previously mentioned tawa) from ungulate herbivory as well as other impacts on the soil microbiome (Bardgett & Wardle 2003). Overall impact of ungulates (deer and goats) on humus pH, leaf litter pH, C and/or N nutrient cycling in leaf litter or soil humus has been found to be variable. Soil carbon storage has shown a variety of responses to deer herbivory in New Zealand suggesting that it slows the transition from grassland to forest though this has not been proven (Wardle et al. 2001, Wardle & Peltzer 2017). From 30 comparison sites, there were significant differences found, but did not point to a single outcome of ungulate impact (Wood et al. 2015). There were significant negative impacts on leaf litter inhabitants, though again, not for all families of invertebrates present (Wardle et al. 2001).

If seed germination is dependent on leaf litter quality, there is the potential for either negative or positive effects from ungulate presence, with reductions in soil porosity (and thus effects on mycorrhizal functioning) and reduction in leaf litter inhabitants being the most likely mechanisms of interaction between ungulates and seed germination identified thus far. This is expected to have some additional effects on the below-ground microbiome as well including seed germination environment, though this process has not been studied.

3.18 Pigs

Pigs (*sus scrofa*) disturb soil to forage, often re-disturbing sites rather than moving to new areas (Parkes et al. 2015). There was evidence that there is a higher ratio of fungi to bacteria in disturbed soils though there was no effect on fungal biomass, which potentially influences microsite suitability for germination (Parkes et al. 2015). Also, pigs may be pre-selecting areas that are already high in fungal activity rather than affecting the microbiome themselves. Overall, the effects of pigs on forest floor habitat were less than expected (Parkes et al. 2015). In terms of effects of gut passage, 14% of eaten matai seeds passed through the gut of two domestic kunekune pigs with 57% of these domestically digested seeds germinating under glasshouse conditions; this is comparable to hand-cleaned seed (O'Connor & Kelly 2012). Of 450 intact matai seeds collected from 3.5 kg of wild pig faeces in Marlborough, 68% germination percentage was reached after 22 months (O'Connor & Kelly 2012). While there is very little information of impact of feral pigs outside of matai seed consumption, it may be supposed that the closely related miro species would react similarly to being eaten.

3.19 Possum

The common brushtail possum (*Trichosurus vulpecula*) prefers to eat fruits and flowers, though leaves make up the bulk of the diet due to availability year-round (Nugent et al. 2000, Nugent et al. 2001). Preferred fruits are miro, *Elaeocarpus* sp, and putaputawētā (Nugent et al. 2001). Catastrophic canopy collapse is sometimes seen within 15 - 20 years of possum colonisation, though high densities of possum are necessary for the most severe dieback situations creating an overall more variable impact on forests when compared to deer (Batchelar 1983, Leutert 1988, Pekelharing & Batchelar 1990, Rose et al. 1992, Payton 2000). By causing canopy destruction and consumption of the reproductive structures of native trees, they likely have larger impacts on seed production and

seed rain patterns which translates into lower germination capacity in possum affected forests, especially for preferred species (kōtukutuku, *metrosideros* sp., kāmahī, Hall's tōtara). Kāmahī is able to regenerate in areas without deer, but with possum. In general, possum impacts are less than deer (Nugent et al. 2001)

Possum and rat control resulted in higher viable fruit and seed production with less damaged fruits, higher amounts of fruits maturing, and a higher amount of fruit eaten by birds that pass the seed unharmed. Partial control resulted in higher fruit production but also more damaged fruits (Dijkgraaf 2002). There were also higher numbers of bird encounters in areas undergoing animal pest control, likely improving the germination benefits associated with bird dispersal of native fleshy-fruited species (Dijkgraaf 2002). Fruit is often available year round in northern NZ, with southern areas low food 'windows' presenting an opportunity to control rodents by introduction of toxic baits (Dijkgraaf 2002).

In addition to accelerating natural senescence, possums may also reduce reproductive output prematurely, either by reducing tree vigour via leaf herbivory or by browsing flowers (e.g., Cowan & Waddington 1990, Bellingham & Lee 2006).

In a controlled feed experiment, possums ate and then excreted 53% of karamū seeds with an average gut passage time of 3.7 days for half of the seeds to pass and 7.55 days for all seeds to pass. Compared to the germination control experiment (4 weeks cool-moist stratification, 24hr soaking in tap water, sown in petri dish with maintained moisture, unheated glasshouse conditions $7.9^{\circ}\text{C} \pm 8.1^{\circ}\text{C}$), passage through possum digestion significantly reduced germination percentage of karamū (70% vs 4% respectively) (Williams et al. 2000). In an experiment by Dungan et al. (2002), there were significant positive effects on possum gut passage for Poroporo (*Solanum laciniatum*, 80% vs 47%) and significantly negative effects on the germination of māhoe (*Meliccytus ramiflorus*, 49% vs 86%). No effect on germination was seen for Ngaio (*Myoporum laetum*) (Dungan et al. 2002). Possums were shown to contribute 17% of all seed collected from field traps suggesting they are an important seed dispersal agent in the New Zealand environment, but this differed between species due to possum preference, contributing <1% of whauwhaupaku and horoeka seed, but 59% of kōtukutuku seed (Dungan 2002). Given that possums can range quite far with home ranges up to 30 ha, possums acting as long distance seed dispersers is a relatively novel interaction with idiosyncratic effects on the germination of native species.

3.20 Rats and Mice

Most rodent effects on germination will come in the form of seed damage via seed predation alongside any damage to fruits before reaching maturity (Ruscoe et al 2004, King 2005). The ecological significance of this impact will depend on whether or not tree population is seed limited or not (Clark et al. 2007). Little consequence would be seen if high seed mortality was experienced naturally. New Zealand has four major introduced rodents: House mice (*Mus musculus*), ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), and kiore (*Rattus exulans*) which are all now seed and fruit predators of tree species (Campbell 1978, Ruscoe et al. 2004, 2005). Of the four rodents studied, mice and kiore are seemingly seed predators in entirety, with ship rats having some potential to disperse small seeds (Williams et al. 2000). There is certainly evidence of increasing numbers of seedlings on islands and in other areas where rats have been eliminated, one of the factors being release from seed predation (e.g. Campbell 2002, Campbell & Atkinson 2002, Clayton et al. 2008). Typically, seed predation exerts a more pronounced impact in situations with limited seed supply, and the predation by exotic mammals can exacerbate seed limitation for species with lower seed production. This phenomenon is particularly evident in larger-seeded species, as post-dispersal seed predation is less likely to affect smaller-seed species, which are more prone to microsite limitations. In a 3-year observational study by Berry (2006), kaikōmako and *Coprosma rotundifolia* experienced high seed predation, leading to significantly increased germination rates when rats and possum were excluded. Conversely, kāpuka, tarata, and kahikatea showed an increase in germination and ongoing presence when mammals were present. This is likely due to reduced competition from other species suffering from seed predation effects. Putaputawētā faced substantial predation by rodents in continuously canopied areas, with *Coprosma rotundifolia* experiencing overall the most significant impact of seed predation (Berry 2006). When examining the interaction between seabirds and rats on germination on offshore islands, rats ate up to 89% of seeds in the study area 5 days with overall germination from soil samples where rats were present resulted in 50% fewer seedlings (Grant-Hoffman et al. 2010).

Mice preferably eat rimu and mountain beech with rats additionally eat miro, though preferential seed predation of rodents is relatively unstudied in New Zealand, with significant data only available for the house mouse dietary preferences on 5 native tree species (Forsyth et al. 2015). Compared to ungulate pressure, mice are predicted to have the largest influence in terms of forest composition by reducing the occurrence of their preferred rimu and mountain beech forage species, causing a change to significant dominance by angiosperms when modelled over a 500-year timeline (Forsyth et al. 2015). Mouse populations are known to increase dramatically following mast year seed production of rimu and southern beech tree species, which only sometimes cause increasing densities of ship rats and kiore (King 1983, King & Moller 1997, Choquenot & Ruscoe 2000, Dilks et al. 2003, Ruscoe et al. 2004, 2005, Harper et al. 2005). Ruscoe et al. (2005) provides calculations for predicting whether or not an entire seed crop can be eaten prior to germination given population numbers as measured in February. Using these calculations Wilson et al. (2007) calculated that a mast seed rain rate for rimu, measured at 1000-1200 seeds per m² in 2003, would escape total consumption for mouse population density of 17-28 per hectare, while non-mast year seed rain rates faced likelihood of total consumption. Of course, germination will correspondingly decrease with the increased amount of seed predation.

Table 8: List of tall woody species where fruit, flower, or seed is eaten by rats (*Rattus* sp.). Adapted from King (2005).

Rat Eaten Tree Species	
nīkau	rewarewa
puka	kanono (<i>Coprosma autumnalis</i> or <i>grandifolia</i>)
karaka	large-seed coprosma
hīnau	taupata (<i>Coprosma repens</i>)
taraire	pūriri
tawa	māhoe
kohekohe	pōkākā
porokaiwhiri	hard beech
tūrepo	kōtukutuku
pōhutukawa	rimu
black beech (<i>Fuscospora solandri</i>)	Hall's tōtara
black maire (<i>Nestegis cunninghamii</i>)	mataī
<i>Nestegis apetala</i>	shining karamū
kawakawa	karamū
karo	tītoki
kahikatea	horopito
miro	kaikōmako

It is extremely unusual for any of the introduced rodents in New Zealand to hoard food, so potential burial increasing germination is an unlikely effect especially at any scale (Vander 1990). Risk of seed predation increased in areas that were dominated by preferred species meaning, for example, that rimu seed predation increased at sites where there were more rimu trees. At sites with greater diversity, seed predation risk was lower. For both rimu and beech trees, seeds that fell further than 15m away from the trunk are most likely to escape predation, showing that intact dispersal mutualisms enhance germination and recruitment capabilities of rodent predated tree species (Wilson et al. 2007).

3.21 Notes on other animals

Seabirds in their nesting colonies increase seed burial and reduce litter via foot traffic and burrowing, also increasing soil surface temperature range, soil perforation, and increase levels of soil nutrient via their droppings and other nesting activities (Bancroft et al. 2005, Fukami et al. 2006, Grant-Hoffman et al. 2010). A comparative 3 year germination experiment was done by Grant-Hoffman et al. (2010) on offshore islands in New Zealand, with a total of 21 islands contributing for leaf litter samples. For islands where rats had been eliminated, high seabird burrow density soil samples had an increase of 20-300% in germination of native plant species, though the seabird trampling caused a negative impact on seedling survival. This further confirms previous evidence that seabird exclusion increases seedling density by Roberts et al. (2007).

A germination study was done via a faecal sample from mallard ducks by Bartel et al. (2018). Unfortunately, the faeces collection was done June and July when many indigenous tree species have already dropped their seed, so it was recommended that this study be recreated in Austral spring to autumn to better understand impact on seed dispersal and germination following duck gut passage for native species (Bartel et al. 2018).

Native Mutualisms and Germination

3.22 Nursery Crops and Allelopathy

Mānuka and kānuka in particular have been shown as being successful as nurse crops to many species. This includes sheltering capacity, light canopy, and preparation of the soil community via mycorrhizal hosting capability (Orlovich & Cairney 2004, Dickie et al. 2012). Native beech species in particular form ecto-mycorrhizal partnerships, which affects the ability of beech to infiltrate previously unoccupied soil.

There appears to be an opportunity to utilise tree ferns, particularly mamaku (*C. medullaris*), as a nursery crop in steep, moist conditions for effective restoration of indigenous shade loving species in comparison to kānuka (Brock et al. 2016, Brock 2017). Under tree ferns, the abiotic germination sites have a more neutral soil pH, lower water deficit, lower ambient temperature, higher levels of soil carbon and nitrogen, reduced competition due to less overall stem density, as well as significantly less light when compared to kānuka (Brock 2017). The species of interest that can regenerate well in a fern dominated canopy are tawa, kohekohe, miro, pukatea, schefflera, and potentially kāpuka (Brock 2017). In terms of inhibiting germination, Enright & Ogden (1987) and Richardson (2005b) provide evidence that in New Zealand tree ferns produce a slowly decaying leaf litter high in nitrogen and alkaloids that potentially suppress seed germination of woody vascular species, proven for kāmahī. Similarly, Brock (2017) observed that the shading effect of ponga/silver fern (*Alsophila tricolor*, formerly *Cyathea dealbata*) has a suppressive effect on conifers. This furthers the evidence that tree fern shading suppresses a selection of native podocarps in particular including tōtara, and Whēki (*Dicksonia squarrosa*) suppressing kahikatea and tarata (Forbes et al. 2016). Given that establishment of later successional trees is difficult under current native afforestation projects, the use of tree ferns as facilitator presents an additional operational pathway in circumstances where these plants are already established or will establish readily.

Tutu is also a well-established, non-replacing nursery crop, especially as it is a nitrogen fixer, which improves native species germination in the natural environment. Study of variably aged tutu stands in Taranaki alongside the increased soil nitrogen were higher organic carbon, higher potential cation exchange capacity, higher magnesium, calcium, and potassium, and greater water holding capacity (Walker et al. 2003). It facilitated

replacement of tutu by kāpuka and in general increased native seed abundance and species richness (Clarkson et al. 2002, Walker et al. 2003). Given that tutu is both poisonous to stock and produced a toxic honey, use of it as a nursery crop may be limited, though its ability to impart increased soil nitrogen makes it a strong species to consider where low-nutrient soil has been identified as a problem (e.g. after an erosion event).

Kauri has been shown to increase the relative fitness of its own seedlings by creating an acidic, dry, low nutrient environment underneath itself (Verkaik et al. 2007, Wyse & Burns 2013). The dominating germination inhibitory effect was due to the low pH caused by kauri leaf litter and was found to negatively affect māhoe (Wyse & Burns 2013). Large-leaved māhoe (*Melicytus macrophyllus*) germination was negatively affected by kauri leaf litter leachate, but not by low pH (Wyse & Burns 2013).

Bryophytes (the non-vascular plant group of mosses, liverworts, and hornworts) have displayed allelopathic interactions with tree species in native forest ecosystems in two studies by Michel et al. (2011a, 2011b). In kōtukutuku germination percentage and radicle growth were negatively affected by leachates made from a moss (*Dendohypopterygium filiculiforme*) and a liverwort (*Lepidoza concinna*) (Michel et al. 2011a). The aforementioned moss had a strong positive effect on the germination ability of māhoe, though radicle growth was prevented (Michel et al. 2011a). *Ptychomnion aciculare* is the most common terrestrial moss found in New Zealand forests and was found to strongly inhibit native tree establishment in areas where it grows thickly in the natural environment (Michel et al. 2011b). Overall, this highlights the need to control bryophytes in controlled germination circumstances, especially when a particular species is not identified as the effect on germination and early root development in particular can be severely negative.

3.23 Indigenous Birds, Lizards, and Insects

Birds are the major co-evolved group of seed consumers in New Zealand. There are three processes by which animal ingestion can affect germination percentage: (1) the fertilisation effect, (2) the scarification effect, and (3) the deinhibition effect (Robertson et al. 2006). All of these mechanisms depend on the passing of unharmed seeds after being eaten. The effects of gut passage and mesocarp removal on native tree seed germination are discussed below.

Effects of mesocarp removal are highly species specific. Impacts on germination of fruit removal versus whole fruit has also been explored for black maire, māhoe-wao (*Melicytus lanceolatus*), and kaikōmako, examining the deinhibition by fruit removal of frugivore gut passage (Robertson et al. 2006). Black maire fruits did not need cleaning or fruit removal via bird for successful germination, fruit removal was essential for kaikōmako which otherwise tended to rot before germination, and māhoe-wao seeds appeared to enter extended dormancy without fruit removal (Robertson et al. 2006). Light abrasion, as would be experienced in the gizzards of New Zealand's ground dwelling birds like kiwi or weka, did not enhance the germination percentage of hīnau nor miro (Carpenter et al. 2018).

Gut passage by kereru improved germination compared to both hand-cleaned seeds and whole fruits of taraire (95.7%, 82.5%, 75% respectively) with the scarification effects being larger than the deinhibition effect (Wotton 2007). Fruit removal and/or gut passage also increased the speed of germination by 1-2 months (Wotton 2007). Trials on miro seed gut passage of kereru produced no difference in germination between whole fruits and defecated seed (Clout & Tilley 1992). Tawa seeds which had passed through the digestive system of kereru may germinate faster than those that do not (Burrows 1999b, Morales et al. 2014). Effects of changes in bird community composition and species abundance on plant reproduction, through pollination and seed dispersal

Weka (*Gallirallus australis*) have been shown to eat more than 26 native fruiting plant species (Clout & Hay 1989). Weka retained seeds in the gut for 2 weeks with seed-filled droppings sometimes being used for nursery production. Weka may be acting as important seed dispersers, with study observing that 93-96% of consumed miro and hīnau seeds being dispersed away from seed parent canopies and approximately 1% being dispersed further than 1 km (Carpenter et al. 2019).

3.24 Lizards

Only two studies have looked at the quality of lizard seed dispersal examining the viability after lizard gut passage (Wotton 2002, Wotton et al. 2016). In the 2002 study, *Coprosma propinqua* seeds digested by the raukawa

gecko germinated at a similar level to both hand-cleaned and whole fruit seeds (Wotton 2002). For kawakawa, lizard digestion had no effect on seed germination ability (Wotton et al. 2016). This is consistent with a meta-analysis of lizard gut passage having no significant effects on germination percentage (Traveset & Verdú 2002).

3.25 Insects

There is very little evidence that tree or ground wētā consume or disperse native tree seeds. Burns (2006) proposed evolutionary interactions based upon a single faecal sample containing seeds of a *Gaultheria* shrub. This theory was further discussed and dismissed as unlikely by Morgan-Richards et al. (2008). Reasons for this were the relatively small size of wētā cibarium (preoral cavity, size ranging from 0.7 - 1.3 mm) making it difficult to consume seeds without damage, the lack of physical dispersal capability, and lack of fruit-seed structure suitable to piecemeal eating that is associated with wētā, and a positive preference shown for eating fruits with larger seeds (Morgan-Richards et al. 2008). Germination was improved for small-seeded kōtukutuku, but consumption by tree wētā destroyed 78% of eaten seeds, the seeds were not physically dispersed, and kōtukutuku fruit was not preferred over the foliage usually eaten (Wyman et al. 2011).

The endemic, nocturnal moth *Cryptaspasma querula*, is known as an obligate seed predator of tawa and taraire. While dispersal away from the seed parent and higher seed density reduced predation, when measured over a seed fall season, over 90% of tawa seed were eventually drilled by the moth larvae. Drilled seed were still able to germinate, but were significantly less likely to be successful than undamaged seeds, showing that larval predation can produce significant negative germination effects on their preferred seeds (Silbauer 2013)

3.26 Invasivity as a clue: NZ woody natives which have become weeds elsewhere

Invasive species, as opposed to their non-invasive counterparts, typically exhibit rapid and/or early seed germination. This tendency is more dominant among invasive species when compared to competing native plants. Overall, this implies that mitigating or avoiding early life-stage competition, achieved by exploiting available germination niches, may provide better outcomes than possessing superior competitive abilities when growing in exotic environments. This idea is reinforced by the observation that invasive species tend to exhibit broader germination cues, especially when in non-native locales compared to native habitats and when compared to their non-invasive competitors. A high germination percentage does not consistently predict invasiveness, potentially implying high seed production and high seed bank presence, rather than high germination rates, is potentially a more effective strategy when invading novel environments (Gioria & Pyšek 2017).

As an area of learning potential cues for improving New Zealand native tree cultivation, Table 4 includes a list of indigenous species that have become weedy elsewhere. Of note are the *coprosma* and *pittosporum* species, which are known to have variable germination in cultivation with or without stratification or other improvement techniques, yet still feature as weedy species internationally. As seen in Table 6 below, the locations where New Zealand tree species tend to be more vigorous are warmer than in their native ranges, suggesting that warm nursery temperatures may increase seed vigour, though additional management of disease or hardening off procedures may be necessary.

Table 9: List of New Zealand native trees that are considered weeds elsewhere (Dawson 2014)

Scientific Name	Location
<i>Coprosma repens</i>	Victoria, NSW, Norfolk Island, Hawai'i, California, South Africa
<i>Coprosma robusta</i>	Southern Victoria, Tasmania, NSW
<i>Cordyline australis</i>	Southern Australia, Northern California
<i>Corynocarpus laevigatus</i>	Hawai'i
<i>Dodonea viscosa</i>	Western Australia

Table 9 Continued: List of New Zealand native trees that are considered weeds elsewhere (Dawson 2014)

<i>Hoheria populnea</i>	California
<i>Leptospermum scoparium</i>	Hawai'i
<i>Metrosideros excelsa</i>	South Africa, Hawaii, Norfolk Island
<i>Myoporum laetum</i>	California, Baja California, Juan Fernández Islands (Chile)
<i>Pittosporum crassifolium</i> , <i>P. eugenoides</i> , <i>P. tenuifolium</i>	South-eastern Australia, Tasmania, Norfolk Island, Hawaii, Isles of Scilly, California, Juan Fernández Islands
<i>Solanum laciniatum</i>	New Caledonia, Hawai'i, western USA (California and Oregon)

3.27 Direct Seeding Update

While nursery production can be more reliable than direct seeding activity, it does require more resources in terms of labour, time, and transport, meaning that it can be a very expensive endeavour. Direct seeding utilises more seed in comparison to planting seedlings and is dependent on the success of a very fragile life stage to create a successful tree establishment, but can result in improved root development for the seedlings alongside lower cost and faster project timelines (Douglas et al. 2007). Direct seeding has had sporadic success across New Zealand, the main challenges being: sourcing sufficient viable seed amounts, uncertainty around optimal sowing time, variability in the duration of the germination timeline, less control on germination conditions and early growth, seed and seedling predation, and specific to many New Zealand situations, the need to control intense vegetation competitive, control of exotic grasses in particular. Success in survival is often limited to early successional species, which are the most likely to survive the germination and early seedling stage without the presence of a nursery canopy (Douglas et al. 2007, Dodd & Power 2007). New technology including drones and designed seed vessels have entered the space, though the overall positive effects of this activity is not yet proven. Below is an update provided on direct seeding activity in New Zealand and discussion of what we know and don't know.

When direct seeding methods of spreading by hand, with a mechanical spreader, by aerial deployment can be considered depending on the accessibility of the site. Use of a bulking agent (such as pumice or sand) will lead to a more even spread of small-seed species, as well as the potential to add beneficial amendments alongside the seed (Douglas et al. 2007, Paul et al. 2020). Seed-to-soil contact is very important for the seeds to germinate properly, with roughening the soil surface with livestock grazing shown to be useful for spring sown seed (Dodd & Power 2007). Dry weather has also been implicated in failure of direct seeding, further emphasising the challenges of determining sowing times as future weather is difficult to predict (Dodd & Power 2007, Douglas et al. 2007, Paul et al. 2020).

A trial carried out on the South Island on bare forest floor Ledgard & Davis (2004), led to successful establishment of mānuka and mountain beech alongside the failure to establish makomako and kāpuka, with grass competition significantly curtailing the overall emergence of native trees. In the Wakatipu basin, direct seeding improved *Coprosma* species emergence, with local, fresh seed further contributing to higher germination rates of all directly sown species in the third year of testing (mānuka, mountain beech, kāpuka, and coprosma) (Paul et al. 2020). Regeneration of black beech was successful in central Canterbury after a near a mature stand of trees was fenced and sprayed, though no additional seed was added (Ledgard et al. 2008). In Northern Canterbury and Banks Peninsula, disturbed soil (using a spade to turn over sods of soil (50 mm deep), leaving bare soil exposed) allowed for the highest emergence in areas of long grass, with herbicide treated areas leading to higher emergence in areas with short grass (Ledgard et al. 2008). Overall, in all long grass treatments, kōhūhū, kāpuka, tī kōuka, kōwhai, and māhoe showed the highest germination rates (16.7%, 10.4%, 8.3%, 7.5%, 2.9% respectively) with kōhūhū, poroporo, kāpuka, tī kōuka, ngaio, and kōwhai showing highest germination rates in short grass (12.9%, 10.4%, 7.9%, 5.4%, 4.0%, 3.8% respectively) (Ledgard et al. 2008). Most of the trials carried out are monitored for a relatively short period, but longer trials see ongoing survival reduce the promising germination rates down to <1-2% over the longer term (Douglas et al. 2007, Ledgard et al. 2008, Paul et al. 2020).

In Waikato hill country, karamu was the only successfully established tree species for both spring and autumnal sowing, with mānuka and tī kōuka also showing successful germinating in autumn but no long-term seedling survival (Dodd & Power 2007). Treading in the seed with sheep, who have a lighter foot pressure and larger mob size than cattle, led to greater germination in spring, but showed no effect in autumn which was likely due to the higher soil moisture levels in autumn already providing the benefit of increased seed-to-soil contact (Dodd & Power 2007).

Broadcast seeding for later successional species (tawa, hīnau and mangeao) were tested in an urban environment by Overdyck et al. (2013), with tawa showing similar germination rates when seed was enclosed in a clay ball or with the fruit flesh removed. Exclusion of seed predators was also shown to have significant effects on tawa germination rates (Overdyck et al. 2013).

Overall, direct seedling is always likely to produce variable results given the strong impacts of annual weather impacts on success. Control of vegetation, consideration of moisture availability, and use of viable seed are likely to produce acceptable results for a small number of pioneer species (kāpuka, mānuka, kōhūhū, and poroporo) in best circumstances given the lower financial cost when compared to seedling establishment.

Part 3: Knowledge Gaps

1. Information on specific soils nutrients influence/effect (outside of nitrogen and phosphorus) on native tree seed germination. What micronutrients affect the embryo development and germination timelines of native tree seed?
2. What are the hormonal fluctuations involved with mycorrhizal symbioses in New Zealand and their potential effects on seed actions?
3. What are the germination interactions of methylobacterium for New Zealand tree species?
4. Are there specific impacts of deer dispersal on tree seed germination and production? What other tree seeds are affected by possum digestion? How much seed do rats and mice eat outside of beech species? What are the dispersal and seed production effects of feral goats (*Capra hircus*)? Which species are most and least palatable beyond the most well studied understory species?
5. What further seed destructive insect species are a threat to native tree seed production and quality? Can improved management decisions around insects or seed collection/storage practices be made?
6. What herbicides or herbicide mixes can be used over young native tree seedlings in a direct seeding application? What is the timeline for application? Can this information be applied to traditional native seedling planting to improve establishment outcomes? There may be opportunity to utilise knowledge held in the nursery sector around use of fungicide or other chemicals as they are applied at very young plant stages.

4. Mātauranga Māori

There is knowledge to be shared between Te Ao Māori and the body of scientific literature that currently exists, especially in the areas of research approach, in the symbolism of Te Reo Māori, and use of multi-media in the transfer of knowledge (Wehi et al. 2009, Mercier 2018, Collier-Robinson et al. 2019). The Treaty of Waitangi is the critical founding document of New Zealand which grants Māori rangatiratanga (chieftainship) over their taonga and ensures that the rights of both Māori and Pakeha are preserved. Māori as the indigenous people also have, “the right to maintain, control, protect, and develop their cultural heritage and traditional knowledge[...], as well as the manifestations of their sciences[...], including seeds, medicines, and knowledge of the properties of fauna and flora species” (Article 31, UN Declaration on the Rights of Indigenous Peoples). Taonga species can be outlined as culturally significant species that shape mātauranga Māori (Māori knowledge) and whakapapa. While whakapapa is usually defined as genealogy, it incorporates the historical, contemporary, and mythical aspects of heritage. This applies not only to people, but to plants, animals, mountains, rivers, and wind and intangible items like identity and knowledge of culture, providing context to the relationships of the natural world through a Māori lens (Tau 2001, Te Rito 2007). The consideration of these wide ranging relationships have definite similarities to western science disciplines like ecology and taxonomy, and thus in combination can lead to unique insights and research considerations which may be overlooked (Hikuroa 2017, Collier-Robinson et al. 2019). Kaupapa Māori (Māori approach) research was developed on several key philosophies or values: whakapapa, whanaungatanga (relationship), manaakitanga (kindness and respect), tikanga (protocol), tohungatanga (expertise), rangatiratanga, and kaitiakitanga (stewardship). Incorporating these values into current research methods involves enhancing local livelihoods utilising local practices to support creation of a research capable workforce, integrating culturally respective practices, and developing proper intellectual rights agreements (Cunningham 2000, Roskrige 2007). When researchers want to work with Māori, whakawhanaungatanga (relationship building) incorporating the wider cultural and linguistic knowledge of kaitiakitanga can facilitate meaningful revitalisation and engagement to more fully conserve or restore the species and ecosystems involved (Collier-Robinson et al. 2019).

Relevant to seeds and germination, there has been increasing collaboration with and participation by Māori in seed conservation in particular following the appearance of kauri dieback disease and myrtle rust as a threat to taonga species. The Māori Biosecurity Network Te Tira Whakamātaki (TTW), which was formalised in 2017 to support biocontrol activities across New Zealand. The majority of these efforts are in support of seed banking of indigenous species, including training, hosting conferences, field monitoring, seed collection aimed at saving seed in both technically and culturally appropriate ways, and the establishment of an Indigenous Seed Bank in Aotearoa (Shadbolt 2023). TTW is also currently developing seed conservation protocols based on best science and mātauranga Māori (Mead 2023, Shadbolt 2023). Most of these seed collection and banking activities are led by the local community and more focused on local whakapapa, rongoa, and trees from oral histories when compared to production nursery practices which focus on pioneer, easily grown, easily stored, and easily sold species (Drummond 2023). In some areas, the work also includes seedling raising activities not only to maintain a living seedbank, but to put the collected species back into the forest. TTW seed collection training aims to work with the local maramataka, which changes with the climate across New Zealand, to ensure iwi are successful in collecting seed suitable for storage and viable germination (Drummond 2023).

Hua parakore is a traditional validation and verification system for mahinga kai (food and goods production) and associated whakapapa for the handling of seeds to return to eating from cultural landscapes, which of course includes many native tree species (Hutchings et al. 2012). Hua parakore is an organic food production assessment framework informed by Māori values and initiated by Te Waka Kai Ora (National Māori Organics Authority of Aotearoa) in 2011. Alongside the western focus on zero chemical inputs or genetic modification to productive plants, it includes attention on saving seed, protection from commodification, indigenous autonomy, and the health of ecosystems, soil and people (Hutchings 2023). Te Waka Kai Ora also has interest in maintaining living seed banks, which requires high amounts of community engagement and understanding of the species, both actions fitting into the ethos of Te Waka Kai Ora seed sovereignty.

Another part of mātauranga Māori to consider as a source for improved seed quality is the Māori lunar calendar (maramataka). The maramataka was developed through a large number of local observations over centuries

and can provide a huge historic insight into forest species productivity, relationship between climatic events and ecosystems, food harvesting locations, and resource management (Anderson 2016, Hikuroa 2017). This indigenous framework is currently being used to establish trees and other plants at the right place and right time to ensure plentiful harvests and to ensure the sustainable supply of seeds (Wai 262 report). The concept of “mauri”, sometimes defined as life force, but more generally described as energy or vibration, is also a relevant idea to inform seed conservation activities and maintenance of seed viability during seed storage activities (Lyver et al. 2019, Tora 2019). Also, the names of locations can provide information on species native ranges (such as Uhi-Mānuka in the Wairarapa, meaning “under the Mānuka trees”) showing what seed resources would be available in different locales or what taonga species could be repatriated to the area (Tora 2019). Myths (pūrakau), stories (kōrero) and proverbs (whakataukī) hold cultural knowledge with potential ecological application, though careful interpretation and contextual understanding are both a necessity and a challenge (Wehi et al. 2009).

Bond et al. (2019) modelled access to two culturally important plant species used for medicinal (rongoa) and weaving purposes, showing how oral records can provide information about range changes of flora, potentially influencing seed collection activity. Knowledge provided by Tūhoe on tawa fruit production assisted in the understanding of more seed production in cool winter conditions, further highlighting the challenges faced by New Zealand’s native tree species in the face of climate change (Clendon et al. 2023). It should also be noted that many nurseries, particularly local community nurseries, are operated by Māori and will hold significant knowledge of germination protocols for tall native tree species.

Research allowing for multicultural outcomes creates an environment for greater involvement with multiple communities and can drive the creation of identity around use of the knowledge generated by the project. There are arguments to be made that human activity has become essential for ecosystem functioning and by allowing cultural practices to inform human use, a sustainable and realistic balance can be restored (Wehi et al. 2009, Wehi & Lord 2017, McAllister et al. 2019). Also, what researchers and land managers sometimes considered “natural” ecosystems are sometimes “cultural” landscapes which have been modified by humans to support a variety of harvesting tasks (Wehi et al. 2009). In general, the access to and practical application of scientific knowledge is an acknowledged weakness for much of generated information. As humans are driven by their identity and relationships within community, creating stronger bonds between the research community and laypeople has the opportunity to establish genuine outreach pathways for knowledge application and form long lasting identity, are responsive to local context, have diverse objectives all based around meaningful knowledge (Lyver et al. 2019, Rayne et al. 2020). When considering the importance of local communities in supporting favourable, long term environmental outcomes, the framework of kaupapa Māori research can provide a desirable pathway to longstanding partnership and action.

Part 4: Knowledge Gaps

1. How can sharing of information around species be facilitated more easily? Help is needed to identify parts of Mātauranga and kaupapa Māori which improve scientific study.
2. How can greater collaboration be encouraged between Māori the scientific community? What are the major roadblocks with deeper community collaboration?
3. What representative organisation would be suitable as a Māori led or partnered group focused on seed science and seed banking?
4. What management structures around taonga species with potential commercial applications need to be in place to support both research and rangatiratanga?

5. In the Nursery

New Techniques, Technology, and Ideas

As the New Zealand native forestry industry grows, there is the expectation that seed and seedling supply will grow to meet demand. Innovation will be required to allow nurseries to produce the wide variety of New Zealand's native trees to the high quality needed for planting projects with more affordability. This section aims to discuss areas of knowledge from outside the native tree industry to provide inspiration and potentially points of collaboration alongside an update on best practices.

5.1 Seed Enhancement Technology

Seed Enhancement Technology encompasses a suite of advanced methodologies designed to elevate the performance and attributes of seeds, with the ultimate goal of optimising their potential during germination and further development. These innovative techniques contribute significantly to modern agriculture by enhancing seed quality, promoting uniformity, and improving overall crop productivity, but have rarely been applied outside of the agricultural sector (Pedrini et al. 2020). Such priming techniques include hydrating seeds in salt solutions (halopriming), solutions of beneficial microbes (biopriming), osmotic solutions (osmopriming), plant hormones solutions (hormonal priming), presence of a magnetic field (magneto-priming), solutions mixed with a solid carrier (matricconditioning), solutions of nanoparticles (nanopriming), hydrating seeds in water (hydropriming), light treatments and plasma processing. Seed coating is another seed enhancement option, wherein seeds are enveloped in protective layers to promote homogeneity of the seed and create easier deployment (Hoose et al. 2019). These coatings can include beneficial microorganisms, nutrients, and substances that safeguard seeds from environmental stressors and pathogens. This protective shield not only shields seeds during the initial stages of germination but also can ensure a more favourable environment for the emerging seedling (Halmer 2008). The majority of these pre-sowing treatments have been explored across a range of crop species rather than forest or native species, often due to a lack of expertise in technique outside of the agricultural field (Pedrini et al. 2018, Pedrini et al. 2020). Significant research would be needed to expand to a wider variety of species and regions. Given the proven improvements to both germination and seedling characteristics for food crops, the potential use of seed priming by nurseries for restoration purposes is tantalising especially when considering the lack of specialised equipment required for the majority of methods. Below, a variety of seed enhancement technologies are discussed to highlight potential application options and observed benefits.

5.2 Priming Via Solution

Soaking seeds in water is a very common pre-sowing treatment as seen in the variety of hot-water or other soaking treatments used. Soaking in water softens and opens the seed coat, increasing the moisture percentage inside the seed, triggering various parts of seed germination to begin. Hydropriming protocols are widely established in the native tree industry with protocols utilising soaking treatments prior to sowing (see Appendix 1).

The use of nanotechnology has recently gained traction in agricultural applications (Sher et al. 2019). There has been exploration of utilising carbon nanotubes to pierce dormant seeds to increase both water and other chemical uptake to break both physical and physiological dormancy. Carbon nanotubes are rolled up seamless cylinders of graphene sheets (Sher et al. 2019), which enter the seed coat through piercing, leading to an increased rate of water absorption. The cylinder can comprise two layers, namely double-walled carbon nanotubes; or it may contain multiple layers, MWCNTs (Sher et al. 2019). Below is a recent description of a carbon nanopriming study done on boreal forest species, rather than crop species.

In this experiment by Ali et al. 2020, a total of 25 buffaloberry (*Shepherdia canadensis* L.) and green alder (*Alnus viridis* L.) seeds were subjected to overnight nanopriming. This priming process involved immersing the seeds in a solution of either 20 µg/mL or 40 µg/mL of carbon nanotubes (CNTs), which were dissolved in deionized water and underwent sonification to ensure proper nanoparticle dispersion. This study revealed that multiwalled carbon nanotubes, functionalized with carboxylic acid (MWCNTs-COOH), outperformed other treatments in promoting germination and growth of healthy seedlings for both upland forest species under examination. It was

proposed that the nanoprimering increased moisture availability across the barrier of the seed coat as well as creating a thicker water layer around the seeds. Notably, a concentration of 20 µg/mL proved highly successful in this regard (Ali et al. 2020). These findings suggest that nanoprimering had a positive impact on seed viability and the germination capacity of seedlings beyond crop species and across a variety of environmental sites.

More specifically for New Zealand, akeake (*Dodonaea viscosa*) has also been the subject of a nanoprimering study by Yousefi et al. 2017 without the carboxylic acid functionalization of the aforementioned study, yet still increasing germination rate as well as ability to germinate under drought stress. This experiment involved 15 hours soaking with stirring, rather than a sonification. The seeds were then dried for 24 hours. After sowing, germination of akeake commenced from day 1, compared to the usual 2-4 weeks using standard scarification protocols (Metcalf 1995). Root biomass was also found to be increased under drought conditions for seeds treated with CNTs. Overall, akeake seeds were able to germinate under all drought stress conditions, with 30 mg/L of CNTs being found optimal for a zero drought stress level. Heightening drought stress levels showed 50 and 100 mg/L of CNTs nanoprimering solution leading to better results (Yousefi et al. 2017).

With significant amounts of seeds in New Zealand having PY or PD, the potential application of carbon nanotubes to both speed germination without stratification and increase ability of seeds to germinate in a wider variety of moisture conditions is a quite exciting research subject for the future.

Haloprimering is a technique where seeds are soaked in some concentration of inorganic salt solution (e.g. CaCl_2 , KNO_3 , NaCl , CaSO_4 , etc). Soaking seeds with nitrate salts, in particular KNO_3 , has shown improvements germination rates, time to germination, and crop yields across several key crop species including: tomato, soybean, sunflower, rice, chickpeas, and corn (Adnan et al. 2020, Khadraji et al. 2020). One of the main uses of haloprimering has been to improve seedling survival in heightened soil salinity conditions (Khan et al. 2009, Jisha & Puthur 2014). Given New Zealand's geographic condition, understanding salinity sensitivity of seeds and having a tool to improve ability to survive hostile salt conditions is likely to be important in evaluating coastal afforestation perspectives as well as restoration potential of other salt affected soils.

Similar to the previous soaking method, Osmoprimering involves the soaking of seeds in non-salt compounds (e.g: polyethylene glycol, plain sugar, mannitol, or vermiculite compounds) (Pedrini et al. 2020). Plants from primed seeds are thought to have improved growth due to increased osmotic adjustment, greater enzyme activation, larger embryo size, and have faster cellular defences when compared to non-primed seed (Martínez-Ballesta 2020)

Bioprimering involves soaking of seeds with beneficial living microbe inoculum, mainly bacterial or fungal agents (Sarkar et al. 2021). As the understanding around plant microbiomes increases, there are increasingly identified applications around supporting plant and soil health for ecosystem restoration (Singh et al. 2023a). This method increases the protection of seeds against soil-borne pathogens and soil pollutants, such as salts and heavy metals, while promoting germination rate and uniformity and can contribute to the restoration of the natural soil microbial community (e.g. Piri et al. 2019, Chakraborti et al. 2022, Singh et al. 2023b). Bioprimering triggers the production of metabolites via an increase in the creation of starch, lipid, and proteins as well as changes in gene expression and the seed's osmotic potential, leading to an overall increase in germination rates, vigour, and root development (Rajput et al. 2021). A combination of *Rhizobium*, *Bacillus* and *Trichoderma* was applied to chickpeas, the mixture gave significantly greater effects than any of the individual isolates with increases in germination, nutrient uptake, plant height, number of branches, nodulation and total biomass (Rudresh et al. 2005). However, in a nursery experiment carried out by Paul et al. (2020), *trichoderma* was found to prevent germination of *kōhūhū*. This highlights the need to recognise species specific interactions for any seed treatment.

As mentioned previously, hormonal priming has traditionally been done with a variety of gibberellins (GA), with 136 GAs having been isolated from plants (Rodrigues et al. 2012). Specifically, GA_3 has been used across a wide variety of species to induce germination. The sole example from New Zealand is the woody shrub *matagouri* in an experiment by Keogh & Bannister (1992). Seed collected from a wild population of *matagouri* had more than 80% germination within 14 days of commencing treatment when chemical scarification (immersion in 98% sulphuric acid for 24 minutes) was followed by imbibition with a solution of 10^{-4} M gibberellic acid for 24 hours. Aeration with fish tank bubbler while at room temperature (20°C) during imbibition with the gibberellic acid solution, resulted in increased germination percentages and rates (Keogh & Bannister 1992). Further exploration of commercially available GA_3 , GA_4 , and GA_7 solutions used as seed pre-treatment for germination across many plant

types seems likely to bear fruit given their wide use in agricultural settings. Also, exploration of both jasmonates and auxins as germination influences may lead to new pathways of controlled germination in New Zealand native trees, specifically conifers, though wider application may be found as well.

5.3 Solid Matrix Priming

Matricconditioning is a seed priming technique in which a solid rather than liquid is the ‘soaking’ medium (i.e. peat moss, charcoal, sand, clay, vermiculite). Sometimes used in conjunction with an additional temperature or stratification method to induce germination. Use of a solid material can also promote survival of plant growth promoting bacteria once applied to the seed, such as the utilisation of bentonite clay to improve bacterial survival after sowing into fine-grained soils (Heijnen et al. 1992). Storage in moist vermiculite has been used in the short term storage of swamp maire with no effect on germination (van der Walt et al. 2021), but also for two *pittosporum* species (tarata and karo) for which germination was increased for populations with initially low germination (Kai et al. 2023).

5.4 Seed Priming via Exposure

Magneto-priming is a more technologically complex and expensive priming method involving exposing seeds to steady or pulsed magnetic fields (MFs) of various strengths. The agronomic application of MFs in plants has shown potential in altering conventional plant production systems by: increasing mean germination rates, root and shoot growth, increasing productivity, increasing photosynthetic pigment content, intensifying cell division, as well as improving water and nutrient uptake (Efthimiadou et al. 2014, Mahajan & Pandey 2014, Menegatti et al. 2019, Serraf et al. 2021). While the mechanisms for these effects are still undefined, application of MF to seeds outside of crops may be a pathway to improve seed germination if other techniques appear to have no effect.

Seed irradiation, particularly utilising gamma rays and potentially x-rays, as a seed enhancement technique has recently gained interest in agronomy as a method to increase seed health, germination rates, and seedling establishment (Araújo et al. 2016). Further study is needed to define the optimal dose, exposition time, alongside other conditions which may impact the priming effect. In New Zealand, this technology is being explored by BioLumic on rice, corn, and soybeans, following evidence of photomorphogenic signalling found within seeds that affect the downstream physiological outcomes (<https://www.biolumic.com/>). While BioLumic is currently focused on crop application, there is the potential to apply this technology to native species in New Zealand.

5.5 Seed Coating as Enhancement

Artificial coating of seed is used to improve handling and for the delivery of protectants, symbiotic microorganisms, micronutrients, soil adjuvants, germination promoters, growth regulators, and colours. In the past decade, there has been significant exploration of seed coating agents to improve a range of seed and seedling factors, again particularly in food and commodity crops (Javad et al. 2022). Some significant factors that contribute to successful coating include porosity, water absorption and holding ability, level of toxicity, porosity, and particle size (Javad et al. 2022). Though, some seeds do require light exposure for germination (e.g. *L. scoparium*), so seed coating is likely to reduce germination percentage, similar to what was found in certain types of perennial ryegrass (Qiu 2020).

The film coating of seed (meaning the coating layer is 5% or less of seed weight) is very similar to certain types of priming which leave a deposit on the seed coat, as a liquid is often used as a depositing mechanism (Pedrini et al. 2017). Film coating has been shown to improve germination under a variety of abiotic challenges. Coating with rhizobia improved germination after low temperature and moisture stress, (Willenborg et al. 2004, Naveed et al. 2014, Rocha et al. 2019a, Rocha et al. 2019b). Coating with a fungal agent, such as *trichoderma* sp. improved seed quality of cumin (Piri et al. 2019) and stimulated root and shoot growth for both maize and canola (Accinelli et al. 2016). Film coating with polymer shows more uncertain improvements with polyvinyl coating reducing oxygen and moisture movement across the seed coat barrier during the germination phase of sugar beet (Duan & Burris 1997). Other commercial polymers improved maize germination after moisture stress alongside improving the movement and protection of seed itself through sowing machinery (Accinelli et al. 2021, Javad et al. 2022), and reducing negative interactions with insecticide leachate on seed performance (Avelar et al. 2012). These polymer

coatings may present a way to improve seed storage capacity by reducing moisture loss for certain recalcitrant seeds and also assist with use of seeding machinery as nurseries scale up tree production. Film coating is usually done with fluidized-bed treaters or pharmaceutical coating drums (Javad et al. 2022, Pedrini et al. 2017).

Seed encrusting is the next step up in terms of mass with the coating in this method ranging from 8-500% of the original seed weight without impacting the original shape of the seed (Pedrini et al. 2017). A binder and target powder are applied to the seed, usually via tumbling drum application. While this technique has larger repercussions for radicle emergence and light sensitive seed, it still presents a way to deliver plant stimulating substances to the sorption zone for a germinating seedling. Cereals in particular seem especially prone to reduced germination outcomes with increasing seed coat thickness (Gorim & Asch 2011, Javad et al. 2022). There is some evidence that plant growth promoting rhizobacteria survives more easily when using an encrusting methodology (Ma 2019). There have also been encrusting trials to explore reducing seed predation by coating with bird or insect repellants like capsaicin (Pearson et al. 2019, Taylor et al. 2020). Activated carbon is another ingredient being explored to improve water retention around the seed or potentially safeguarding seed against herbicide applications (Madsen et al. 2014)

Seed pelleting is this thickest coating application, with the original size and shape of the seed being fully obscured (Pedrini et al. 2017). This method encounters the greatest impact on emergence, but can also deliver the largest amount of material to a germination site. In a New Zealand study direct seeding experiment, clay balls were shown to improve the germination and survival of tawa, but otherwise are relatively untested (Overdyck 2013).

Though seed coating has not been widely explored with New Zealand native tree species in particular, there could be improvements identified for recalcitrant seeds, for species which require specific mycorrhizal inoculant, for nursery automation, and for direct seedling applications. Care would need to be taken to ensure coating does not negatively impact specific species germination requirements.

New Nursery Germination Technology

5.6 Transplanting (a.k.a. Pricking Out)

Seeds often start in seed trays or germination beds before getting moved to their final root trainer or pot to increase space and nutrients as needed to finish the grow-out period prior to sale. Beyond the need for increased space, transplanting also addresses variability of seed germination and seedling health leading to later gaps in the production line of the nursery (Grift et al. 2008). This ‘pricking out’ step involves the transfer of young seedlings from high density seed trays to low density containers and is often done manually. This presents a step which is high in labour time and costs and may produce variable outcomes due to individual worker judgement and ability.

The first automated transplanter for vegetable production was designed by Kutz et al. in 1987 and claimed a 90% success rate for seedling transplantation. The first transplanter with plant analysis capabilities was designed in 2001 and judged the health of the seedling via leaf colour (Ryu et al. 2001). True machine vision technology (MVT) started to be incorporated in prototype transplanters in 2008 by Jiang et al., with further improvements including root positioning being analysed as well (Syed et al. 2019). Visual identification of the leaf is essential for the functioning of the transplanter for both automated movement of the seedling as well as for identification of healthy individuals. With the improvements in image analysis capability and processing power, modern automated transplanting systems often identify and move seedlings with greater than 95% accuracy against pre-selected morphological characteristics and potentially transplanting up to 35,000 seedlings per hour (Syed et al. 2019, viscongroup.eu).

Again, as like many other seed technologies, much of the research has been restricted to crop species. Current application to New Zealand tree species production would need research into: specific recognition algorithms not only for species but also for healthy seedlings, better transplant sensors to improve grasping and handling, research into proper machine grip strength and depth, and exploration of standardisation of nursery equipment to facilitate automation. The transplanting of seedlings should be done in groups of the same age where germination is variable, which will be important for some native tree species given their germination habits. Also, the young seedlings should be moved to the grow out container as soon as is feasible to reduce change of transport shock and damage to larger root systems as they are for older seedlings (Vinosh et al. 2021). There is the potential to incorporate hyperspectral imaging technology as used in precision agriculture, which has shown the ability to

identify individual native species, plant disease monitoring, weed competitiveness, and has been used to assess a variety of fruit qualities to a high degree (e.g. Feng 2022, Lou et al. 2022, Wieme 2022).

5.7 Production of Native Woody Species as Forestry Grade or Bare Rooted

There has been some research done on production of native New Zealand tree and shrub species as bare-rooted, as is the open-ground production of *Pinus radiata*. While not strictly germination, there is the potential to reduce costs of native seedlings if open-ground, bare-rooted seedling production can be applied utilised. Open-ground production research was done by Dr. David Bergin and Cemino Cole in conjunction with Taupo Native Plant Nursery. Karamū in particular did well with open ground production, transport, planting and survival, with open-ground tī kōuka surviving better than those seedlings produced in root trainers. Koromiko had similar survival across PB3, root-trainer, and open-ground seedlings. Mānuka as a bare-rooted seedling had similar survival to root-trainer seedlings, but lower survival than those raised in PB3 bags. Overall, this suggests that there is potential for this type of seedling production to apply to some native woody species, but there is little real-world data (SFF Report, Mahurangi Magazine).

5.8 Disease Management in the Nursery Setting

Given the benefits of mycorrhizal inoculant for plant growth, utilisation of fungal inoculation within the nursery production pipeline will improve seedling survival for trees out in the field (Dickie et al. 2012). The incorporation of mycorrhiza as early as possible in seedling growth can also reduce fungal pathogens (Williams et al. 2010). Usually, these fungi are incorporated at the pricking out stage, so including the amendment earlier in seed beds is proposed to add to the realised benefits (Williams et al. 2010, Dickie et al. 2013). Commercial inoculant products appear to not be effective colonisers of native trees, so nurseries should engage in collection from forest soils with the target tree species (Williams 2010). When collecting arbuscular mycorrhizae, soil should be gathered down to 20cm. When collecting ectomycorrhizae, duff at the soil surface should be gathered (Williams 2010). For the growth of southern beech (Nothofagaceae) ectomycorrhizal fungi is critical. Creation of effective inoculant is necessary for proper infection, but has been explored by Bohorquez et al. (2021). To ensure viability, it is recommended that fruiting bodies of ECF are dried at 30°C, then be freshly prepared as a suspension in water when inoculation of the seed trays occurs (Bohorquez et al. 2021). Cool storage at 4°C has been shown to be beneficial for Hysterangiaceae ‘Motatapu’, though further application to other mycorrhizal species is necessary (Bohorquez et al. 2021).

Trichoderma is a soil fungal species thought to protect seeds from pathogenic fungi (Paul et al. 2020). It was shown to impede germination of Kōhūhū, though it improved root and shoot growth in some cuttings of New Zealand natives (*Pittosporum*, *Lophomyrtus*) (Paul et al. 2020).

5.9 Improved Germination Protocols

With native afforestation becoming more important to sustainable land use in New Zealand, smart germination protocols will create success for nurseries to supply not only early successional species but those species which are more naturally rare, require more sheltered habitats, explore native timber production species, or face risk of extinction from disease or other threat.

Below are some general points to consider for nursery production of native trees taken from Hill (2004).

1. Fresh is best
 - a. Fresh seed, meaning seed produced and collected in the same year as sowing, usually germinates more quickly than old seed. Most New Zealand native seeds ripen between February and May. Seed is recommended to be sown no later than the following spring after collection.
2. Gentle seed handling
 - a. Undamaged seeds germinate better. Avoid damaging seeds by handling fruits gently when collecting. Keep drying time and temperatures (where applicable) as low as possible. Proceed

through cleaning protocols as gently as possible (i.e. slow down tumbling/sieving equipment).
And protect freshly collected seed from extreme temperatures.

3. Clean seed appropriately to produce high seedlot quality
 - a. Removal of debris, empty and damaged seed can assist with sowing success, and prevent future gaps in the nursery production line. Cleaning methods include hand sorting, liquid floatation (bad seeds often float), aspirators or fans to remove chaff, gravity separators to find heaviest seed, sieving to remove rubbish and/or small immature seeds, and wet or dry tumbling for scarification.

Much of the development of New Zealand native tree germination using a standard protocol was done in the Burrows (1993, 1994a, 1994b, 1995a, 1995b, 1995c, 1995d, 1996a, 1996b, 1996c, 1996d, 1996e, 1997, 1999a and 1999b) and is previously summarised in the germination reviews in 1991 (Fountain and Outred), 1994 (Bannister & Jameson), and 2007 (Rowarth et al.). Below is a list of updated species germination protocols and information from beyond 2007. The protocols highlighted below are updated protocols available in the post-2007 published literature or were not previously summarised. Most compared a variety of germination treatments from which the most successful was identified. A full list of tall tree species germination protocols is provided in Appendix 1.

Table 10: List of native New Zealand tree species with published improvements to storage or germination protocols since previous germination literature review (Rowarth et al. 2007) or were not discussed previously.

Species	Methodology	Reference
Tawa (<i>B. tawa</i>)	Removal of fruit in combination with tawa leaf leachate treatment significantly increased germination speed with more than 70% of germination occurring within 2 weeks compared with under 30% without leachate. Without fruit removal, leachate treatment still significantly increased germination percentage (above 80% versus above 30%), but germination took significantly longer (4 months). Tawa leaf leachate concentration was a 50:1 liquid made from 100g of leaves in 1L of water.	Morales 2015
Tarata (<i>P. eugenoides</i>), Karo (<i>P. crassifolium</i>)	Low temperature stratification at 4°C for 8 weeks or more resulted in almost full germination of tarata seeds (87-93%) but had no effect on <i>P. crassifolium</i> seeds (75% fresh vs. 68% stored). Drying of seeds reduced germination significantly for both species. Use of moist vermiculite when storing will assist in maintaining germination rates of fresh seed (at 20°C for <1 month) or assist in improving tarata germination if initial percentage is low.	Kai et al 2023
Swamp maire (<i>S. maire</i>)	Make sure to collect ripe fruit as ripe seed produces more robust seedlings (though stage 2 unripe fruit is still viable). Removal of fruit will improve germination rate and percentage (98% vs 23%). Germination percent for fresh seed at 15/25°C rather than 20/30°C was marginally better and had lower fungal contamination (98 vs 95%). Maximum seed storage longevity (8 weeks without germination) was obtained by mixing fruits with vermiculite in airtight containers stored at 5°C.	Van der Walt et al. 2021

Tawari (<i>I. brexioides</i>)	Removal of fruit will increase germination percentage (75% vs 8%). Burial of fruit will increase germination percentage (75% vs 50%). Shade may or may affect germination, but make sure to keep the soil moist. Germination started 1 month after collection.	Thomson 2013
Akeake (<i>D. viscosa</i>)	Untreated seeds had low final germination 30%. Seeds that had been acid-scarified (97% H ₂ SO ₄), immersed in boiling water (10min) or exposed to 50°C (1min) all achieved 91% subsequently when incubated at 25°C, though successful germination occurred from 5-25°C. Germination was inhibited above 30°C. Scarified seeds become more sensitive to salinity	Al-Namazi et al. 2020
Mountain beech (<i>F. cliffortioides</i>)	Cold-moist stratification increased germination to 21.7% from 5.3% found in untreated seeds. Most germination occurred within 1 month. Cold dry stratification had germination percentage of 3.3% and did not break dormancy. <i>Nothofagus</i> require sheltered microsites for germination.	van Galen et al. 2022
Kauri (<i>A. australis</i>)	Germination of fresh seed occurs at temperatures above 11 °C, but rates are highest between 19- 27 °C. Secondary forest temperatures, thin leaf litter, and light (as under mānuka or kānuka canopy) proved most favourable for field germination	Steward & Beveridge 2010
Ramarama (<i>L. bullata</i>)	Seed collected in June germinated within 10 days, with maximum germination rates reached in 6 weeks. 100% germination was achieved with fresh seed. This suggests that cold winter temperatures broke dormancy. Dry-cold stratification reduced germination to 74%. Germinated at 15/25° C with a 18 h photoperiod	van der Walt 2022
Rōhutu (<i>L. obcordata</i>)	Germination of 85% and 82.5% for fresh and stratified seed respectively. Germinated at 15/25°C with a 18 h photoperiod.	van der Walt 2022
Rōhutu (<i>N. pedunculata</i>)	Stratification is required. Wet stratification (in fruit pulp) at 5°C for 4 weeks stimulated germination (38%) with significantly higher germination after 20 weeks of wet stratification (72%).	van der Walt 2022
Hall's tōtara (<i>P. laetus</i> , formerly <i>P. cunninghamii</i>)	Ex-agricultural arbuscular mycorrhizal fungi (AMF), commercially bought, resulted in significantly reduced <i>P. cunninghamii</i> shoot growth. Forest AMF, collected, caused a significant increase in both <i>P. cunninghamii</i> root production and root concentrations of P compared with ex-agricultural AMF	Williams et al. 2010
Marsh ribbonwood (<i>P. divaricatus</i>)	On salinity sensitivity. Between 0.5% NaCl and 3.5% NaCl, differences in salt sensitivity were noted. 0%NaCl = 78% germination, 0.25%NaCl = 63% germination, 0.5%NaCl = 24% germination. Viability falls off to 2% or lower at higher rates of salt application to soil.	Partridge & Wilson 1987

Pūriri (<i>V. lucens</i>)	1 fruit sown per cell in potting mix. Trays were kept in dark room. The temperature was then set to 7°C, and trays were watered to keep the media damp for 12 weeks before being transferred to a glasshouse maintained at 22 ± 3°C. Germination started 6 weeks after cool stratification. 40% successful germination, an additional 30% identified as still dormant and viable	Southward et al. 2002
Hutu (<i>A. lucida</i> var. <i>lucida</i>)	Fresh seed was collected, the fruit removed and was sown into a standard potting mix in a shaded greenhouse with overhead watering. Temperatures were between 14 - 32°C. Germination began at week 5 and finished week 13 to week 19 depending on the collection site. Lowland population had an average germination percentage of 32%, while the submontane population had an average germination percentage of 76%.	Martin & Ogden 2002
Mountain Lacebark (<i>H. glabrata</i>)	Cold moist stratification at 4°C for 42 days lead to a peak in germination at 20°C, though germination near freezing temperature is possible for this species. After stratification, at 20°C there was 50% germination in 9 days.	Haase 1987

5.10 Notes from International Sources

Given the difficulty in improving controlled germination, there is the potential to apply new protocols from international exploration of similar species. The research below has been done on species from the same genus as tall native tree species from New Zealand. There is the potential for those producing seedlings to try new methodology to improve germination rate or percentage. No published literature was found using these methods on New Zealand species.

Genus *Nothofagus* (Southern Beech in New Zealand)

There is evidence that treatment with a solution of gibberellic acid can break the state of internal dormancy of the seeds in some *Nothofagus* species in Mediterranean environments (Cabello 2004; Cabello et al. 2016; Rocuant 1984; Santelices et al. 2011). Previous work has shown that either cold stratification or gibberellic acid treatments can improve seed germination of related species including *Nothofagus macrocarpa* (A. DC.) Vasq. & Rodr. (Cabello et al. 2016). Treatment with a solution of thiourea, a chemical promotor of germination (Baskin and Baskin 2014), has also been recommended to break the dormancy of seeds but its effectiveness in overcoming the latent dormancy in some *Nothofagus* is unclear.

N. glauca: Germinated at 20°C without light (Cabello et al. 2019)

Treatment 1: 60 days stratification only (wet sand, 5°C) - 95% germination

Treatment 2: Seeds soaked in GA₃ 800 mg/L for 24 hr - 97% germination

Treatment 3: Seeds soaked in Thiourea 7.5g/L for 24 hr - 92% germination

As southern beech species in New Zealand usually require cold-moist stratification for a minimum of 1 month to break dormancy, the possibility of seed treatments bypassing this period would allow seeds to be utilised more quickly if collected late, or to produce larger seedling by planting season due to the extra month of growth.

Genus *Myoporum* (Ngaio in New Zealand)

Ruiz et al. (2017) found that scarification of *Myoporum montanum* significantly increased germination percentage from approximately 22% to 86% after being warm-moist stratified at 25/35°C for 4 weeks. The seeds also responded well to warm-moist stratification, but this was after 6 months of dry storage at 3°C, which may or may not have had an effect on dormancy.

Genus *Alectryon* (Tītoki in New Zealand)

The fleshy arils of *Alectryon Oleifolius* seeds were removed and had best germination percentage (76%) when sown at spring temperatures of 25/15°C. Complete seed coat removal also led to higher germination (86.5%). (Ruiz-Talonia et al. 2022).

Genus *Elaeocarpus* (Hīnau, pōkākā in New Zealand)

This genus of trees is notoriously difficult to germinate, with multiple species facing less than 5% regeneration in the wild, with germination of New Zealand's hīnau recorded as taking up to 7 years to germinate (Khan et al. 2003, Yang et al. 2001, Ramasubbu & Irudhyaraj 2016, Carpenter et al. 2018). Research into this genus has increased since the discovery of certain indolizidine alkaloid compounds and their potential use in treatment of diseases like cancer, diabetes, and potentially AIDS (Iralu et al. 2018).

Cracking of the seed coat, soaking in hot water, and various priming via solid matrices have shown to be effective in increasing germination in this genus. For *Elaeocarpus prunifolius*, cracking the seed coat significantly promoted germination (46%) and increased germination rate with a mean germination time of 146 days (compared with approximately 24% and 213 days for the control treatment). Cracked seed followed by soaking the seeds with a mixture of both 200 mg/L GA₃ and KNO₃, however, increased the germination to 31% and reduced mean germination time to 56 days (Iralu et al. 2018).

5.11 Seed Storage and Recalcitrance

Recalcitrance is another challenge to seed viability and future germination with a global estimation of 3% of species producing seeds that are sensitive to desiccation (recalcitrant) and, consequently, are not suitable for conventional seed storage or banking methods (Wyse & Dickie 2017, Ballesteros et al. 2021). Seeds that can survive drying and freezing processes for storage purposes are called 'orthodox' or desiccation tolerant (Wyse et al. 2023). Currently the only seed bank in New Zealand for indigenous species is the New Zealand Indigenous Flora Seed Bank (NZIFSB) at the Margot Forde Genebank Centre and administered by AgResearch, the Plant Conservation Group, and Massey University. The NZIFSB only holds approximately 65 species of tall native trees which can be accessed by researchers, though available seed quantity varies greatly depending on species.

Many New Zealand native trees are known to produce recalcitrant seeds, with taller species that produce heavy, fleshy fruit more likely to fall into the non-orthodox category (Wyse et al. 2023). Wyse et al. (2023) also found that dispersal mode was the most influential aspect of woody species in predicting production of orthodox or recalcitrant seeds (with animal dispersal being most likely to show recalcitrance). Overall, for woody species in New Zealand, 81% are thought to produce orthodox seed, 17% are likely to have intermediate or recalcitrant seed, with the remaining 1% having insufficient data to determine (Wyse et al. 2023). Recalcitrant seed production was also more common in the warmer, northern region New Zealand than in cooler, temperate regions, which is a pattern observed globally (Wyse et al. 2023, Wyse & Dickie 2018).

Most species with physical dormancy, with the associated hard seed coat, are able to be dry stored for longer periods of time. An example being *Sophora* (Kōwhai sp.) seed from across New Zealand, Chile, and Hawai'i showing 40% germination even after 24-40 years of storage (Norton et al. 2002). Small seeds in hard capsules, such as mānuka, kānuka, rewarewa, and pōhutukawa can also be dry stored for a period of time prior to sowing (Hill 2004). Testing showed that coastally collected *Pittosporum* seed is more sensitive to desiccation given the different climatic impacts of climate on inland versus coastal population locations (Kai et al. 2023). Both karo and tarata are thought to be recalcitrant, with storage in moist vermiculite assisting with maintaining seed viability for a relatively short storage period (Kai et al. 2023).

Sowing fresh seed for New Zealand native species is a well-known method of germination, with many trees losing viability quickly (e.g. Kauri). *Syzygium mairi* is an example of storage not being possible for longer than 8 weeks due the necessity of maintaining seed moisture (Van der walt 2022). Rehydration in ascorbate solution has increased survival after desiccation in other species. Both of these aforementioned species are of particular interest in term seed storage given the risk of disease (Kauri dieback and Myrtle rust) to their ongoing long-term presence in their natural ranges (Wyse et al. 2023).

In general, current advice states that orthodox seeds of New Zealand tree species should be stored at 5-9% moisture in tins, thick plastic bags, drums, or aluminium foil pouches at 5°C, with thick-walled containers keeping out as much air as possible. Recalcitrant seeds should be treated with a fungicide, then mixed with untreated sawdust or vermiculite and stored in sealed plastic containers (Hill 2004). A convenient rule of thumb is that addition of storage temperature and relative humidity should not exceed 70 (i.e. 15°C and 50 percent relative humidity, 15+50 = 65) (Hill 2004). For seeds that are unable to be stored, living collections are essential for maintaining ongoing seed accessibility.

See Appendix 3 for Seed Storage Behaviour of New Zealand Native Tall Woody Species.

Part 5: Knowledge Gaps

1. Seed storage methodology for recalcitrant seeds. Exploration of cryopreservation or living collections may be viable pathways.
2. Potential application of seed priming technology to native tree species. Seed pre-soaking outside of water-priming is extremely limited for native tree species. There is the potential to explore dormancy alleviation, increase germination percentage, and/or increasing germination rate.
3. The usefulness of seed coating and the effects on germination of native trees requires more research. There may be applications in direct seeding, germination improvement and seed handling in nursery automation.

6. Conclusion

Native trees play a crucial role in maintaining ecological balance, yet their germination encounters formidable challenges arising from habitat degradation, invasive species competition, and the impacts of climate change. The successful germination of native tree species is paramount for the restoration of their populations, biodiversity, and overall preservation of ecosystem health, especially considering further challenges presented by changing climate. To effectively address these challenges, a thorough understanding of the germination process is essential, encompassing factors such as seed production, viability, dormancy, and the identification of optimal growing conditions.

In the context of New Zealand's native tall trees, the exploration of germination has transcended conventional protocols, offering profound insights into the intricate natural processes that contribute to the regeneration of native forests. Beyond established methodologies, there is a growing opportunity to enhance germination outcomes by adapting agricultural practices and expanding knowledge concerning lesser-known species. Delving into issues related to population genetics, dispersal mechanisms, and mutualistic relationships holds promise for refining germination protocols, particularly in the strategic planning of seed collection and preparation.

As the native forestry industry in New Zealand continues to expand in scale, innovative applications of insights derived from the natural world present alternative pathways for expanding native forest cover. Approaches, such as direct seeding, offer promising avenues beyond traditional seedling production methods. Recognizing the intrinsic value of New Zealand's native trees as essential components of the nation's natural heritage underscores the importance of their successful germination for long-term ecological sustainability.

Mitigating challenges, advancing research efforts, and fostering community engagement are pivotal components of ensuring the successful restoration and preservation of native tree populations. By amalgamating existing practices with avant-garde methodologies, New Zealand can solidify its commitment to environmental stewardship and biodiversity conservation, securing a flourishing future for its native tree flora. This concerted effort not only contributes to the resilience of New Zealand's ecosystems but also exemplifies a model for sustainable conservation practices worldwide.

6.1 Recommendations

Germination, being a major stage in seedling production, needs a strong science foundation to increase seedling supply, reduce costs, and improve native reforestation outcomes. High quality seed and good practices are essential to making the production of native trees viable on a larger scale. The knowledge gaps at the end of each section provide research questions for consideration in the future. More general recommendations to improve the germination landscape and seed science in New Zealand are below:

1. Complete an evaluation of current and expected native tree seed demand compared to current seed supply and collection mechanisms active in the marketplace. This will assist in identifying regions and species of interest as well as gaps in supply or management of seed supply that is needed.
2. Look for opportunities to support collaborative research between agricultural seed science and native tree science. Crop species have led the way in terms of seed science research and expanding this to a wider range of species will be part of the leading edge of restoration practice. There is incredible knowledge of high-quality seed production, seed management, germination enhancement, and seed handling that can provide improvement to native seedling production and other afforestation projects.
3. Establishment of a wider indigenous plant and tree seed banking infrastructure in partnership with Māori. Consideration should be made around seed banking as a 'back-stop' (conservation) vs as a source for propagation (use by industry). This presents an opportunity to engage with communities who are familiar with native tree diseases, motivated to maintain genetic diversity, and interested in a wide array of native species beyond commercial application. Inspiration for a living collection similar to the Te Kohinga Harakeke o Aotearoa – National New Zealand Flax Collection may be a viable option for some species.

4. Establishment of a database of seed collection locations for researchers would assist in accessing seed for experimental purposes. This could also contain facilitated pathways for Māori partnership into research through established relationships. There is an opportunity to use tree resources located on public land or to create a value pathway for landowners with established native forest.
5. Establish protocols and templates for appropriate sourcing of native seeds for commercial or restoration applications. This includes processes around genetic evaluation, site access and permitting, and seed certification, or support establishment of seed orchards. This could also include a more centrally held document library of up-to-date species recommendations for regional restoration activities. Sustainable management and use of seed resources will be essential making sure seed production areas are not overharvested nor exploited by private commercial interests.
6. Further explore nursery production requirements and pain points to enable adoption of technology and increase ability to meet growing native tree seeding demand in the forestry market. Investment in or incentives to improve nursery infrastructure will create opportunities for smaller regional nurseries to grow and provide tech-based employment while increasing seedling supply and, ideally, reducing costs.

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Appendix 1 - Native Tree Germination Protocols

New Zealand native tall (can grow >5m in height) species propagation protocols. Protocol references are: Burrows (1990s), Hill (2004), Metcalf (2007), Wardle & Platt (2011). Cool-moist stratification requires temperatures between 0-6°C and is usually done in the refrigerator (which is usually 4°C). Seeds can be soaked for several hours, then placed into a plastic bag or tub with a moist, not wet, cloth or paper towel to maintain moisture levels. Seed can also be sown into moist raising mix or vermiculite, then refrigerating the bag or tray for the required time. Make sure moisture is maintained throughout the stratification period.

Scientific Name	Common Name	Propagation
<i>Acakama rosifolia</i> , <i>A. nubicola</i>	Makamaka	Sow seed fresh. Seed becomes ripe in March or April.
<i>Agathis australis</i>	Kauri	Sow fresh seed, ideally within 10 days of collection. Press seeds into firm raising mix and lightly cover. Usually within 1 month germination of fresh seed occurs at temperatures above 11°C, but rates are highest between 19- 27°C. Seed does not store well.
<i>Alectryon excelsus</i>	Tītoki/ NZ Ash	Fresh seed is best and no pre-treatment is required though 4 weeks cool-moist stratification can even out germination rate. Removal of the fleshy aril may increase germination percentage, but is not necessary. Cover only lightly. Germinate in intermediate to warm conditions.
<i>Aristotelia fruticosa</i> , <i>serrata</i>	Mountain Wineberry, Makomako/ Wineberry	Fresh seed should germinate within two months with removal of fruit. Otherwise cool-moist stratify for 3-4 weeks and germination should occur within 1 month of sowing. Intermediate conditions recommended for germination. Seeds store well.
<i>Ascarina lucida</i>	Hutu	Fresh seed with the fruit removed is recommended. Germinate in a shaded greenhouse with overhead watering. Temperatures were between 14 - 32°C. Germination began at week 5 and finished week 13 to week 19 depending on the collection site.
<i>Avicennia marina</i> subsp. <i>australasica</i>	Manawa, NZ Mangrove	Can be grown from establishing plantlets or by germinating seed. Maintain moist conditions at all times and improve success by spraying raising trays monthly with salt water.
<i>Beilschmedia tarairi</i>	Taraire	Best if sown fresh, but 4 week stratification may even the germination rate. Removal of fruit flesh is recommended but not necessary. Press fruit into raising mix, do not cover the seed with mix, and treat for weevils. Place clear plastic or glass over the seed tray and place in a warm, moist, shady spot. Sowing individually will allow for easy handling later.
<i>Beilschmedia tawa</i>	Tawa	Collect cast seed from the ground and use the float method to eliminate non-viable seed. Removal of fruit in combination with tawa leaf leachate watering significantly increased germination speed with more than 70% of germination occurring within 2 weeks compared with under 30% without leachate. Without fruit removal, leachate treatment still significantly increased germination percentage (> 80% versus >30%), but germination took significantly longer (4 months). Tawa leaf leachate concentration was a 50:1 liquid made from 100g of leaves chopped and soaked in 1L of water, then used to water seed trays every 4 days. Similar protocol may apply to taraire, but has not been tested.
<i>Brachyglottis</i> sp.	e.g. Rangiora, Puheretaiko, Rautini	Sow fresh seed as seed loses viability quickly. Germination is usually best in shady positions, cool to intermediate conditions, and kept moist. Cuttings are more reliable.
<i>Carmichaelia</i> sp.	Pink Tree Broom, Weeping Tree	Make sure to collect ripe seed. Germination from fresh, ripe seed is usually easy. Older seed will likely need a hot water treatment of 50°C and left for 12

	Broom, Tainoka, <i>C. muritai</i>	hours. Some species may need a warmer 70°C treatment.
<i>Carpodetus serratus</i>	Putaputawētā/ Marble leaf	Cool-moist stratify for 6 weeks, then sow. Removal of fruit flesh may be helpful. Germination should occur in 4-6 weeks.
<i>Coprosma</i> sp.	e.g. Māmāngi, Kanono, Karamū, Taupata, Glossy Karamū	Sow fresh or with fleshy fruit removed. 2-4 week cool-moist stratification is usually recommended. The seed does not store particularly well. <i>C. lucida</i> and <i>C. robusta</i> germinate best when exposed to light.
<i>Cordyline australis</i> , <i>C. banksii</i> , <i>C. indivisa</i>	Tī kōuka, Tī ngahere, Tōī	Freshly sown seed takes approximately 2 months of germinate. Sow thinly in the bed as seedlings are susceptible to mould if too crowded. Cool-moist stratification for 4-6 weeks can speed germination.
<i>Coriaria</i> sp.	Tutu species.	Usually sown fresh, though seed can store well. Remove flesh from around seed, which is an inhibitor. Cool-moist stratification for 4 weeks will even out the germination rate. Germination should occur within 1 month. There are claims that seeds sown in May in particular will germinate within 1 month, otherwise germination may take 9-12 months.
<i>Corokia cotoneaster</i>	Korokio, Mountain Corokia	Sowing fresh seed is recommended. Can be cool-moist stored for 2 months to potentially even out germination rate. Germination can take upto 12 months. Potentially scarification followed by 1-2 month cool-moist stratification is helpful.
<i>Corynocarpus laevigatus</i>	Karaka	Sow fresh seed in intermediate to warm conditions. 1 month cool-moist stratification is possible, though seed does not store well. Half-buried (meaning pressed into raising mix, but not covered) sowing method is recommended, as well as sowing into individual cells for easy handling. Treat with insecticide to prevent maggot infestation. Germination should occur within 6 weeks. Seedlings are deep-rooted and do best in deep containers.
<i>Dacrycarpus dacrydioides</i>	Kahikatea/white Pine	Sow fresh or cool-moist stratify for 4-6 weeks. Lightly cover sown seed and moisten seed bed thoroughly. Young germinants are susceptible to damping off, so fungal management is recommended. Seed stores reasonably well.
<i>Dacrydium cupressinum</i>	Rimu	Cool-moist stratify for at least 6 weeks. Freezing the seed or seed trays (or placing in a frosty area) aids germination. Keep trays in a shady area. Take care not to damage the sensitive tap root when pricking out. Seed stores reasonably well.
<i>Didymocheton spectabilis</i>	Kohekohe	Sow fresh seed by pressing into raising medium and place in intermediate to warm conditions. Very susceptible to fungal disease so treatment with a suitable fungicide before and after sowing is recommended.
<i>Dodonaea viscosa</i>	Akeake	Untreated seeds had low final germination 30%. Seeds that had been acid-scarified (97% H ₂ SO ₄ , 1-5min, then rinsed clean), immersed in boiling water (10min) or exposed to dry heat of 50°C (1min) with all treatments achieving 91% germination when subsequently incubated at 25°C, though successful germination occurred from 5-25°C. Germination was inhibited above 30°C. Scarified seeds become more sensitive to salinity. 2 week cool-moist stratification prior to heat treatment can even the germination rate. Seed stores well.
<i>Dracophyllum arboreum</i> , <i>D. latifolium</i> , <i>D. traversii</i>	Tarahinau, Neinei/ Spiderwood, Mountain Neinei	Sow fresh from seed collected in March or April. Germinate in cool to intermediate conditions. Can be difficult to keep alive in hot conditions. Seedlings are very slow growing and require control of moss/liverwort to avoid smothering.
<i>Elaocarpus dentatus</i> ,	Hīnau, Pōkākā	Sow seed in firm raising mix, cover lightly, water well and leave to drain. These

<i>E. hookerianus</i>		species have very slow and/or erratic germination sometimes taking 3-5 years. Stratification protocols are unproven. Potential piercing or puncturing of woody endocarp should be explored.
<i>Entelea arborescens</i>	Whau	Easily grown from seed, with warm conditions or placing in a glasshouse making easier and faster germination. Germination occurs quickly after seed is placed in 90°C water and left to cool, and then sown. Seed stores well.
<i>Fuchsia excorticata</i>	Kōtukutuku	Sow ripe seed, which depending on locality occurs between Oct-February. Cool-moist stratify for 2 weeks prior to sowing. As seeds are very small, mix with some of the raising mix for ease of sowing. Germinate in cool to intermediate conditions and bring into light when seedlings appear. Damping off can be a problem, so suitable fungicide use is recommended. Seed stores well.
<i>Fuscospora cliffortioides</i>	Mountain Beech/ Tawhairauriki	Cold-moist stratification for 1 month increased germination to 21.7% from 5.3% found in untreated seeds. Most germination occurred within 1 month. Optimum stratification times can vary between seedlots, but are generally between 4-6 weeks. Cold dry stratification was not effective. Seed can be stored up to 8 years in air-tight containers if seed moisture is between 8-10% of oven dry weight and kept between 5-10°C.
<i>Fuscospora fusca</i> , <i>F. solandri</i> , <i>F. truncata</i>	Red Beech, Black beech/ Tawhairauriki, Hard Beech/ Tawhairaunui	Cool-moist stratify seeds for 1 month prior to sowing. Germinate in intermediate conditions. Optimum stratification times can vary between seedlots, but are generally between 4-6 weeks. Seed can be stored up to 8 years in air-tight containers if seed moisture is between 8-10% of oven dry weight and kept between 5-10°C.
<i>Griselinia littoralis</i>	Kāpuka, Broadleaf	Cool-moist stratify seeds for 6 weeks after collection in late autumn. Seedlings are susceptible to fungal attack, so sow sparingly. Seedling roots are easily damaged, so handle carefully. Seed does not store well.
<i>Griselinia lucida</i>	Akapuka, Shining Broadleaf	Cool store seed in moist peat for 2 weeks prior to sowing. Seedling roots are easily damaged, so handle carefully. Seed does not store well.
<i>Halocarpus bidwillii</i> , <i>H. biformis</i> , <i>H. kirkii</i>	Bog pine, Pink pine	Follow rimu protocol: Cool-moist stratification for at least 6 weeks. Freezing treatment may aid germination. Place seed trays in a shady position. Germination can be slow.
<i>Hedycarya arborea</i>	Porokaiwhiri	Sow fresh seed or cool-moist store for up to 3 months if storage is necessary. When sown fresh and under protection, germination should occur within 2 months, otherwise they tend to germinate in autumn.
<i>Hoheria angustifolia</i> , <i>H. populnea</i> , <i>H. sextylosa</i>	Narrow-leaved Houhere, Houhere, Lacebark	Seed should germinate readily after 4 weeks of cool-moist stratification. Germinate in intermediate to warm conditions. Seeds can be infected by caterpillars, so collect them early or dust with insecticide.
<i>Hoheria glabrata</i> , <i>H. lyallii</i>	Mountain Lacebark/ Whauwhi	Cool-moist stratify for 2-3 months prior to sowing. Germinate in intermediate to warm conditions. Seeds can be infected by caterpillars, so collect them early or dust with insecticide.
<i>Ixerba brexioides</i>	Tawari	Removal of fruit will increase germination percentage (75% vs 8%). Burial of fruit will increase germination percentage (75% vs 50%). Keep the soil moist, with warm conditions recommended. Germination started 1 month after collection.
<i>Knightia excelsa</i>	Rewarewa	Store seeds somewhere warm and dry so capsules open and release seed. Cool-moist stratify for 2 weeks prior to sowing. Sow into a tray with mixed fungicide and cover seeds only lightly. Warm conditions are required for a good germination rate. Place in a shaded greenhouse or partly shaded location. Seedlings are susceptible to fungal disease.
<i>Kunzea ericoides</i>	Kānuka	Store seeds somewhere warm and dry so capsules open and release seed. Sow

		fresh seed by pressing into medium and only cover very lightly, if at all. Some recommend cool-moist stratification for 3 weeks prior to sowing, but it should not be necessary. germination should occur within 2 weeks. Seed stores well.
<i>Laurelia novae-zelandiae</i>	Pukatea	Store seed capsule in a paper bag in a warm dry place until seed is released. No need to remove seed fluff. Germination can be aided by 2 weeks of cool-moist stratification. Keep trays moist. Seed does not store well for any length of time and should be sown fresh.
<i>Lepidothamnus intermedius</i>	Yellow Silver Pine/ Mountain Pine	Cool-moist stratify for 1-2 months prior to sowing. Germinate in cool conditions. Germination is unknown. If problems are encountered, try rimu protocol.
<i>Leptospermum scoparium</i>	Mānuka	Store seeds somewhere warm and dry so capsules open and release seed. Sow when fresh by pressing seed into medium without covering, but well watered. Light exposure helps with germination. Germination should occur within approximately 10 days. Seed stores well.
<i>Libocedrus bidwillii</i> , <i>L. plumosa</i>	Pāhautea, Kaikawaka	Sow fresh or cool-moist stratify for 4 weeks. Stratified seed should germinate within 2 weeks. Germinate in cool to intermediate conditions.
<i>Litsea calicaris</i>	Mangeao	Remove fruit flesh and cool-moist store for 4-6 weeks. Germinate in warm conditions. Avoid overwatering. Seedling roots are easily disturbed/damaged, so avoid transplanting too many times.
<i>Lophomyrtus bullata</i>	Ramarama	Seed collected in June germinated within 10 days, with maximum germination rates reached in 6 weeks. 100% germination was achieved with fresh seed. This suggests that cold winter temperatures broke dormancy. Dry-cold stratification reduced germination to 74%. Germinated at 15/25° C with a 18 h photoperiod. Seedlings are prone to fungal disease.
<i>Lophomyrtus obcordata</i>	Rōhutu	Germination of 85% and 82.5% for fresh and stratified seed respectively. Germinated at 15/25°C with a 18 hr photoperiod. Seedlings are prone to fungal disease, so a fungicide treatment regime is recommended.
<i>Lophozonia menziesii</i>	Silver Beech	Cool-moist stratify seeds for 1 month prior to sowing. Germinate in intermediate conditions. Optimum stratification times can vary between seedlots, but are generally between 4-6 weeks. Seed can be stored up to 8 years in air-tight containers if seed moisture is between 8-10% of oven dry weight and kept between 5-10°C.
<i>Melicope ternata</i>	Wharangi	Seed should germinate easily when sown early and fresh, but success can be variable. Germinate in cool to intermediate conditions in a partially shaded position.
<i>Melicytus lanceolatus</i> , <i>M. ramiflorus</i>	Narrow-leaved Māhoe/Māhoe Wao, Māhoe	Remove fleshy fruit, wash seed in running water for a minimum of 6 hours and cool-moist stratification for 4-6 weeks prior to sowing. Sow sparingly into raising mix.
<i>Meryta sinclairii</i>	Puka	Sow fresh seed. Keep moist during germination. Seed does not store and only remains viable for a short period of time.
<i>Metrosideros sp.</i>	Akatea, Pōhutukawa, Aka, Northern Rātā	Sow fresh seed promptly as it does not store. Water well and allow to germinate in shady, warm conditions.
<i>Metrosideros umbellata</i>	Southern Rātā, Ironwood	Cool-moist stratification for 6 months will aid germination. Best if sown into sphagnum moss and left uncovered or very lightly covered. Seed stores well unlike other <i>Metrosideros</i> .
<i>Mida salicifolia</i>	Maire Taiki/NZ Sandalwood	This is a semi-parasitic tree and little information is available on propagation. It is known to depend on hemi-parasitic attachments to the host plant to survive alongside having normal roots.

<i>Myoporum laetum</i>	Ngaio	Easily raised from seed. Some suggest scarification of 2-3 month cool-moist stratification prior to sowing. Germinate in intermediate conditions.
<i>Myrsine australis</i> , <i>Myrsine sp.</i>	Mapou/ Red Matipo, Toro, Kermadec Mapou	Cool-moist stratify for 4 weeks or dry store for 3 months prior to sowing. Germinate in cool to intermediate conditions. Germination can be unreliable taking 2-18 months.
<i>Neomyrtus pedunculata</i>	Rōhutu	Stratification is required. Wet stratification (in fruit pulp) at 5°C for 4 weeks stimulated germination (38%) with significantly higher germination after 20 weeks of wet stratification (72%).
<i>Nestegis apetala</i> , <i>N. montana</i>	Coastal Maire, Narrow-leave Maire/Oro oro	Coastal: Sown fresh seed will germinate following spring. Oro oro: Sown fresh seed will germinate over 2-3 years. Germinate in warm conditions. Can try cool-moist stratification for 2-3 months prior to sowing or cutting off the end of endocarp (being careful to not damage the embryo) then sowing fresh. Germination is likely to be low, slow, or erratic.
<i>Nestegis cunninghamii</i> , <i>N. lanceolata</i>	Black Maire, White Maire	After collection, soak fruit to remove outer pulp. Cool-moist stratify for 20 weeks prior to sowing.
<i>Olearia sp.</i>	Tanguru, Akepiro, Small-leaved Tree Daisy, Akiraho, Heketara, Coastal tree daisy	Sow fresh seed. Sowing in September is recommended. Sow using the 'scree method' using small stones or grit as covering material over standard raising mix. Germinate in cool to intermediate conditions and keep moist, but well-drained. Germination is often hit or miss with cuttings being more reliable.
<i>Pennantia corymbosa</i>	Kaikōmako	Sow fresh and germinate in cool to intermediate conditions. Cool-moist stratification for 1 month may assist in evening germination rate. Potential to store at 4°C storage for up to 4 weeks. Seedlings often germinate in July. Known to have issues with seed rotting.
<i>Phyllocladus sp.</i>	Tanekaha/Celery Pine	Cool-moist stratify for 2-3 months and germinate in cool conditions. Germination is erratic. Seedlings usually appear in spring. Seed can be difficult to collect with high seed years being relatively rare, potentially 1 good year every 10.
<i>Piper excelsum</i> <i>subsp. excelsum</i>	Kawakawa/ Pepper tree	Sow fresh seed after mashing fruit and removing pulp. With bottom heat applied, germination should take 4-6 weeks. Otherwise, provide warm summer conditions. Seedlings are susceptible to fungal disease.
<i>Pisonia umbellifera</i>	Parapara	Seed should be sown fresh and germinated in a sheltered position, ideally in a greenhouse.
<i>Pittosporum sp.</i>	Rautawhiri, Karo, kōhūhū, Haekaro	Trees easily hybridise, to take care to collect from isolated groups (cutting propagation is most common due to ease and to avoid hybrids). Removal of sticky substance from seed is recommended. General rule is cool-moist stratify for 6 weeks to even the germination rate. Germinate in cool to intermediate conditions. Germination is likely to be erratic and/or slow. Seed stores well.
<i>Pittosporum crassifolium</i>	Karo	Easy from seed (germination may be slow. Semi-hardwood cuttings also viable.
<i>Pittosporum eugenoides</i>	Tarata/ Lemonwood	Low temperature stratification at 4°C for 8 weeks or more resulted in almost full germination of tarata seeds (87-93%). Use of moist vermiculite when storing will assist in maintaining germination rates of fresh seed (at 20°C for <1 month) or assist in improving tarata germination if initial percentage is low.
<i>Plagianthus regius</i>	Manatu/ Ribbonwood	Cool-moist stratify for 4 weeks prior to sowing and germinate in a cool place. Press covering material down firmly to ensure good seed-soil contact and water thoroughly. Seed should be dusted with insecticide if stored to avoid grub infestation.

<i>Planchonella costata</i>	Tawāpou	Sow seed after 4 weeks of cool-moist stratification. Germinate in intermediate to warm condition.
<i>Pectinopitys ferruginea</i>	Miro	Sow fruit buried approximately 10mm. Place the seed tray in a shady location will mimic forest conditions and discourage weed growth. Germination takes up to 2 years or sometimes longer.
<i>Podocarpus acutifolius</i> , <i>P. laetus</i> , <i>P. totara</i>	Needle-leaved Tōtara, Mountain Tōtara, Tōtara	Cool-moist stratify for 4-6 months prior to sowing. Germinate in cool to intermediate conditions. Germination usually occurs within 6 weeks, but can be an erratic occurrence for up to 1 year.
<i>Prumnopitys taxifolia</i>	Mataī	Sow ripe fruit buried approximately 5mm. 3 month cool-moist stratification will lead to 50% of seed germinating in 6 months. Otherwise, germination is erratic and can take up to 5 years.
<i>Pseudopanax arboreus</i> , <i>P. colensoi/ternatus</i> , <i>P. crassifolius</i> , <i>P. laetus</i> , <i>P. ferox</i> , <i>P. lessonii</i> , <i>P. linearis</i>	Whauwhaupaku, Three-finger, Horoeke, Houpara, Fierce Lancewood, Mountain Lancewood.	Remove fruit or seed capsules. Soaked in tap water for 24 hr, 12:12hr light period, 20C with 20% relative humidity = 76% germination. Seed should germinate well after 6 weeks of cool-moist stratification. Can also try covering the seed tray with clear glass or plastic sheet and place in a warm shady place. Seedlings can be susceptible to leaf spot disease, so use of a suitable fungicide is recommended.
<i>Pseudowintera colorata</i>	Horopito	Sow fresh or cool-moist stratify for 2 months prior to sowing. Germinate in cool conditions. Germination can take up to 2 years.
<i>Pterophylla racemosa</i> , <i>P. silvicola</i>	Kāmahi, Towai	Seed is quick to disperse, so harvesting must be planned carefully. Store seed capsules in a warm dry place until seed is released. Sow seed fresh. Watch out for moss smothering as seedlings grow quite slowly. Perhaps 6 month storage of seed is possible.
<i>Quintinia acutifolia</i> , <i>Q. serrata</i> , <i>Q. elliptica</i>	Kumarahou/ White Birch, Tāwheowheo/ NZ Lilac	Cool-moist stratify for 4 weeks to even out germination rates. Germinate in cool to intermediate conditions.
<i>Raukaua edgerleyi</i> , <i>R. simplex</i>	Raukawa, Haumakoroa	Collect ripe seed and cool-moist stratify for 6 weeks. Germination tends to be slow.
<i>Rhopalostylis sapida</i>	Nīkau Palm	Fresh seed in fruit should germinate readily, though can take up to 1 year. Warm germination conditions should assist greatly in speed. Prick out soon after germination. The seed coat will remain attached to germinant for approximately 1 year. Seed stores well.
<i>Schefflera digitata</i>	Pate/ Seven-Finger	Make sure seed is ripe when collected. Seed soaked in tap water for 24 hr, 12:12hr light period, 20°C with 20% relative humidity led to 70% germination. Cool-moist stratification for 1 month will even out germination rate. Pate seedlings respond well to fertile soil and should be kept moist and frost-free.
<i>Solanum aviculare</i> , <i>S. lancinatum</i>	Poroporo	Sow fresh seed and germinate in intermediate to warm conditions. Germination should take 1-2 months
<i>Sophora microphylla</i> , <i>S. tetraptera</i>	Kōwhai, Large-leaved Kōwhai	Fresh green seed can be sown without pre-treatment. Older seed requires scarification (clip seed coat), hot water (77-90°C, let soak for 48 hrs), or acid soak treatment (concentrated sulphuric or battery acid for 10-15 mins). Germinates better when sown outside of the winter season.
<i>Streblus banksii</i> , <i>S. heterophyllus</i>	Ewekuri, Tūrepo/Milk Tree	Sow fresh or cool-moist stratify for 2 weeks prior to sowing. Germinate in intermediate conditions. Seed stores well.
<i>Syzygium maire</i>	Swamp maire	Ripe seed produces more robust seedlings (though stage 2 unripe fruit is still viable). Removal of fruit will improve germination rate and percentage (98% vs 23%). Take care not to damage seed during fruit removal. Germination percent for fresh seed at 15/25°C rather than 20/30°C was marginally better and had

		lower fungal contamination (98 vs 95%). Make sure the seed does not dry! Soaking seed for several days prior to sowing can drown invading insects if present.
<i>Toronia toru</i>	Toru	Sow fresh seed. Cool-moist stratify for at least 6 weeks. Seed can take up to 2 years to germinate. Germinate in cool to intermediate conditions. If problems persist, physical scarification or hot water treatment may help.
<i>Vitex lucens</i>	Pūriri	Sow fresh and germinate in a shady position. Can cool-moist stratify for 4 weeks after removal of fruit pulp. Germinate in intermediate to warm conditions.

Species in Particular Need of Germination Protocol Improvement

1. *Beilschmiedia tarairi* - Potential to use tawa leachate method to improve.
2. *Coriaria* sp. - Germination is known to be variable, taking 9-12 months
3. *Corokia* sp. - Protocol suggests cool-moist stratification of 2-3 months, with germination still taking up to 12 months.
4. *Dracophyllum* sp. - Protocol suggests that from fresh seed, germination takes up to 12 months.
5. *Elaeocarpus* sp. - germination is slow and erratic, known to take 3-5 years.
6. *Halocarpus* sp. - No specific germination protocol as 'rimu protocol' is recommended and germination is noted to be slow.
7. *Hoheria* sp. - Protocol suggests cool-moist stratification for 2-3 months before sowing.
8. *Lepidothamnus* - Protocol suggests cool-moist stratification for 1-2 months prior to sowing, with germination of an unknown timeframe.
9. *Metrosideros umbellata* - Protocol suggests cool-moist stratification for 6 months prior to sowing.
10. *Melicope ternata* - Germination success known to be variable.
11. *Mida salicifolia* - Germination protocol is unknown.
12. *Myrsine australis* - Protocol suggests cool-moist stratification for 2-3 months prior to sowing, with germination still taking 2-18 months.
13. *Nestegis* sp. - Protocol suggests 20 week cool-moist stratification or germination taking up to 3 years.
14. *Phyllocladus* sp. - Protocol suggests cool-moist stratification for 2-3 months prior to sowing, with germination still erratic.
15. *Pittosporum* sp. - Some species known to have super erratic germination.
16. *Podocarpus* - Protocol suggests cool-moist stratification of up to 6 months prior to sowing, with germination still erratic.
17. *Pectinopitys ferruginea* - Germination known to take 2 years or longer.
18. *Prumnopitys matai* - Germination known to take 3-5 years, regardless of treatment.
19. *Toronia* - Germination known to take up to 2 years.

Appendix 2 - Seed Dormancy Classes

Dormancy Classes of tree and shrub families found in New Zealand.

This is a list of New Zealand native woody flora families taken from a global assessment of the dormancy types found across different plant families. Data from Willis et al. 2014. No Dormancy (ND), Physiological Dormancy (PD), Physical dormancy (PY), Morphological Dormancy (MD), Morphophysiological Dormancy (MPD), Physical+Physiological Dormancy (Combo).

Family	Plant Type	ND	PD	PY	MD	MPD	Combo
Araucariaceae	Gymnosperm	0.70	0.30				
Cupressaceae	Gymnosperm	0.15	0.85				
Podocarpaceae	Gymnosperm				0.21	0.79	
Acanthaceae	Dicotyledon	0.55	0.45				
Alseuosmiaceae	Dicotyledon		1				
Amaranthaceae	Dicotyledon	0.16	0.84				
Araliaceae	Dicotyledon				0.18	0.82	
Argophyllaceae	Dicotyledon	Not analysed					
Asteraceae	Dicotyledon	0.22	0.78				
Atherospermataceae	Dicotyledon	0.17	0.17			0.67	
Campanulaceae	Dicotyledon	0.07	0.42		0.17	0.35	
Chloranthaceae	Dicotyledon					1	
Coriariaceae	Dicotyledon	0.60	0.40				
Corynocarpaceae	Dicotyledon		1				
Cunoniaceae	Dicotyledon	0.33	0.66				
Elaeocarpaceae	Dicotyledon	0.11	0.81				
Ericaceae	Dicotyledon	0.13	0.81				
Euphorbiaceae	Dicotyledon	0.37	0.63				
Fabaceae	Dicotyledon	0.21	0.02	0.77			
Gesneriaceae	Dicotyledon	0.60	0.40				
Griselinaceae	Dicotyledon	0.67	0.33				
Lamiaceae	Dicotyledon	0.16	0.84				

Lauraceae	Dicotyledon	0.35	0.64	0.01			
Loganiaceae	Dicotyledon	0.27	0.73				
Loranthaceae	Dicotyledon	0.50	0.50				
Malvaceae	Dicotyledon	0.39	0.08	0.50			0.02
Meliaceae	Dicotyledon	0.58	0.42				
Monimiaceae	Dicotyledon					1	
Moraceae	Dicotyledon	0.70	0.30				
Myrtaceae	Dicotyledon	0.50	0.50				
Nanodeaceae	Dicotyledon	See Santalaceae					
Nothofagaceae	Dicotyledon	0.21	0.79				
Nyctaginaceae	Dicotyledon	0.27	0.73				
Oleaceae	Dicotyledon	0.17	0.78			0.05	
Onagraceae	Dicotyledon	0.31	0.69				
Paracryphiaceae	Dicotyledon						
Pennantiaceae	Dicotyledon	Usually dust seeds					
Piperaceae	Dicotyledon	0.41	0.32		0.14	0.14	
Pittosporaceae	Dicotyledon		0.03		0.07	0.90	
Plantaginaceae	Dicotyledon	0.15	0.85				
Polygonaceae	Dicotyledon	0.46	0.54				
Primulaceae	Dicotyledon	0.21	0.79				
Proteaceae	Dicotyledon	0.29	0.71				
Rhamnaceae	Dicotyledon	0.11	0.29	0.29		0.31	
Rosaceae	Dicotyledon	0.09	0.91				
Rousseaceae	Dicotyledon					1	
Rubiaceae	Dicotyledon	0.34	0.64		0.01		
Rutaceae	Dicotyledon	0.24	0.75	0.01			
Santalaceae	Dicotyledon		0.17		0.06	0.78	

Sapindaceae	Dicotyledon	0.39	0.42	0.18			0.01
Scrophulariaceae	Dicotyledon	0.19	0.81				
Solanaceae	Dicotyledon	0.13	0.87				
Strasburgeriaceae (*Escalloniaceae)	Dicotyledon				0.33	0.67	
Thymelaeaceae	Dicotyledon	0.27	0.73				
Urticaceae	Dicotyledon	0.50	0.46	0.04			
Violaceae	Dicotyledon	0.22	0.78				
Viscaceae	Dicotyledon	See Santalaceae					
Winteraceae	Dicotyledon				0.14	0.86	
Arecaceae	Monocotyledon	0.01			0.15	0.84	
Asparagaceae	Monocotyledon	0.07	0.24		0.06	0.63	
Overall prevalence (%)		13.53	27.18	1.8	1.52	10.81	0.03
Dormancy Type		ND	PD	PY	MD	MPD	Combo

Appendix 3 - Seed Storage Behaviour

Seed Storage Behaviour of Tall Woody Species of New Zealand (Adapted from Wyse et al. 2023). Orthodox meaning seed can be dried and stored long-term. Intermediate meaning seed is somewhat sensitive to desiccation, but shorter term storage is possible. Recalcitrant meaning that seed is sensitive to desiccation so alternative seed/genetic storage methodology is required.

Scientific Name	Common Name	Seed Storage Behaviour
<i>Ackama rosifolia</i>	Makamaka	Intermediate
<i>Agathis australis</i>	Kauri	Intermediate
<i>Beilschmiedia tarairi</i>	Taraire	Unknown
<i>Beilschmiedia tawa</i>	Tawa	Recalcitrant
<i>Brachyglottis rotundifolia</i>	Pūtawharetāiko, muttonbird scrub	Unknown
<i>Coprosma arborea</i>	Māmāngi	Unknown
<i>Coriaria arborea</i>	Tutu	Orthodox
<i>Dacrycarpus dacrydioides</i>	Kahikatea	Recalcitrant
<i>Dacrydium cupressinum</i>	Rimu	Intermediate
<i>Didymocheton spectabilis</i>	Kohekohe	Recalcitrant
<i>Elaeocarpus dentatus</i>	Hīnau	Recalcitrant
<i>Fuchsia excorticata</i>	Kōtukutuku	Orthodox
<i>Fuscospora cliffortioides</i>	Mountain beech, Tawhairauriki	Orthodox
<i>Fuscospora fusca</i>	Red beech, Tawhairauriki	Orthodox
<i>Fuscospora solandri</i>	Black beech, Tawhairauriki	Orthodox
<i>Fuscospora truncata</i>	Hard beech, Tawhairauriki	Unknown
<i>Griselinia littoralis</i>	Kāpuka	Recalcitrant
<i>Halocarpus biformis</i>	Pink pine	Unknown
<i>Ixerba brexioides</i>	Tāwari	Recalcitrant
<i>Knightia excelsa</i>	Rewarewa	Orthodox
<i>Kunzea sp.</i>	Kānuka	Orthodox
<i>Laurelia novae-zelandiae</i>	Pukatea	Recalcitrant
<i>Lepidothamnus intermedius</i>	Yellow silver pine	Unknown

<i>Leptospermum scoparium</i>	Mānuka	Orthodox
<i>Libocedrus bidwilli</i>	Kaikawaka	Orthodox
<i>Lophozonia menziesii</i>	Tawai, silver beech	Orthodox
<i>Macrolearia colenso</i>	Tupare, leatherwood	Unknown
<i>Manoao colensoi</i>	Manoao, silver pine	Unknown
<i>Melicytus ramiflorus</i>	Māhoe	Orthodox
<i>Metrosideros robusta</i>	Northern rātā	Orthodox
<i>Metrosideros umbellata</i>	Southern rātā	Orthodox
<i>Olearia avicenniifolia</i>	Mountain akeake	Unknown
<i>Pectinopitys ferruginea</i>	Miro	Orthodox
<i>Phyllocladus toatoa</i>	Toatoa	Unknown
<i>Podocarpus totara</i>	Tōtara	Recalcitrant
<i>Prumnopitys taxifolia</i>	Mataī	Orthodox
<i>Pseudopanax arboreus</i>	Whauwhaupaku, five finger	Recalcitrant
<i>Pterophylla racemosa</i>	Kāmahi	Orthodox
<i>Pterophylla silvicola</i>	Towai	Intermediate
<i>Quintinia serrata</i>	Tāwheowheo	Unknown
<i>Rhopalostylis sapida</i>	Nīkau	Orthodox
<i>Sophora chathamica</i>	Kōwhai	Orthodox
<i>Vitex lucens</i>	Pūriri	Orthodox