

Seeding for native afforestation in the temperate New Zealand forests

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Abstract

New Zealand supports rich temperate forests believed to have occupied up to 80% of its land area below climatic tree line prior to human arrival in the 11th century, but deforestation, particularly motivated by conversion to agricultural systems in the last 150 years, has decreased today's forest cover to less than 30% of the original estimate. There is currently interest in relatively large-scale afforestation of degraded lands, and this has initiated research and development to improve seeding of native forest species. We provide a synthesis of available literature, ongoing research, and practical experience to identify critical aspects of candidate afforestation sites, summarize practices and techniques used in current seeding research and operations, and recognize factors that affect success or failure of seeding native species. The main challenges are that pastoral farming has dramatically altered the soil microbiome, non-native mammalian herbivores and weeds reduce seedling establishment success, and many native trees are mast seeding or have recalcitrant seeds. Selection of sites with predictably adequate rainfall, deployment of fast germinating pioneer species, procurement of high-quality seed, availability of appropriate soil symbionts, and post-establishment weed and animal control are all important components of success when seeding native forest species in New Zealand.

Keywords

forest restoration, direct seeding, direct drilling, ECM, AMF, masting

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1 Forests ecosystem of New Zealand

1.1 Physiographic region

The New Zealand archipelago comprises three main islands (*Te Ika o Maui*¹ North Island, *Te Wai Pounamu* South Island, and *Rakiura* Stewart Island, Figure 1) and numerous smaller islands lying mainly between latitudes 34.42° S and 47.28° S with a land area of more than 268,000 km². The climate is oceanic subtropical to temperate with a mean annual temperature of 16 °C in the north and 10 °C in the south. Much of New Zealand receives between 600–1600 mm rainfall annually. However, mountain ranges throughout North and South Islands intercept the predominant westerly winds to create dramatic west–east rainfall gradients. This is especially noticeable on the South Island where annual rainfall to the west of the Southern Alps can exceed 10,000 mm but some inland eastern areas receive less than 300 mm. In line with global trends, the New Zealand landmass has warmed by 0.9 °C in the last century, and 2021, 2022, and 2023 have been the hottest years on record. Climate change scenarios for New Zealand based on IPCC 6th assessment models predict temperature increases of up to 3.0 °C by 2090, an increase in severity and frequency of drought, and more extreme rainfall events (Ministry for the Environment 2024).

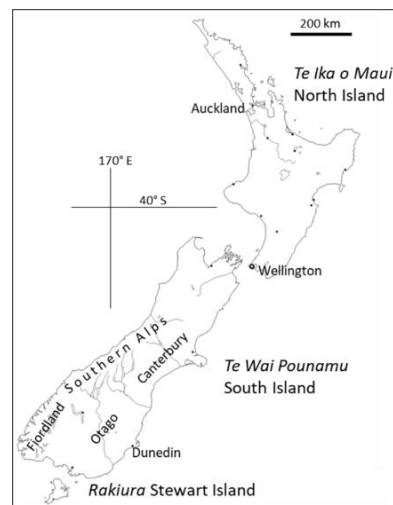


Figure 1. Map of New Zealand showing locations mentioned in the text.

¹ Indigenous Te Reo Māori place names in italics

1.2 Forest types

Prior to human arrival in the 11th century up to 80% of New Zealand's land area below climatic tree line was likely covered to some extent with conifer (Gymnosperm) and/or broadleaved (Angiosperm) forests. New Zealand native trees are overwhelmingly evergreen, unlike northern hemisphere temperate forests; only a handful of native broadleaved trees, and none of the native conifers, are deciduous. Forest composition and structure are strongly affected by elevational, latitudinal, and topographical effects on rainfall and temperature, as well as the legacy of Pleistocene glaciations on species distributions. Conifer-broadleaved forest dominated by kauri, *Agathis australis* (D. Don) Loudon (Araucariaceae), is restricted to northern North Island, along with a number of remnant representatives of tropical families. In North Island and high rainfall South Island forests, members of the Gondwanan conifer family, Podocarpaceae, are often emergent over a diverse broadleaved canopy made up of species in families such as: Araliaceae, Cunoniaceae, Elaeocarpaceae, Lauraceae, Malvaceae, Myrtaceae and Pittosporaceae. These forests also support an abundance of ferns, vines, and epiphytes, making them structurally more similar to tropical rainforests than northern hemisphere temperate forests. Evergreen forests of *Fuscospora* and *Lophozona* species (southern beeches, Nothofagaceae) dominate in drier and colder parts of New Zealand, as well as extremely high rainfall areas such as Fiordland, often growing in near monoculture. Prior to the arrival of humans, fire was not a frequent occurrence; the most common disturbances were likely windthrow, flooding and landslides, with geothermal activity and volcanism affecting central parts of North Island (Veblen et al. 2016).

1.3 History of deforestation and degradation

Like the rest of the world, human activities in New Zealand have resulted in large scale deforestation such that < 30% of pre-human forest cover remains today (Ewers et al. 2006). Unlike the rest of the world this deforestation has occurred in little more than 800 years, as New Zealand was the last major landmass to be permanently inhabited by humans. Losses have accelerated over the past 150 years, during which time half of the land area below the tree line has been converted into agricultural systems. Furthermore, New Zealand is unique among temperate forested lands globally in that native forests did not evolve with grazing mammals; the only mammals native to New Zealand are marine mammals and bats (suborder Microchiroptera). A large suite of introduced mammalian grazers, browsers, and seed predators have become naturalized in native forests following the arrival of humans (King 1990), causing considerable ecological damage (e.g., Wilson et al. 2006). These species include seven species of deer (Family Cervidae), feral pigs (Family Suidae), feral goats, chamois and Himalayan Tahr (all Family Bovidae), Australian brush-tailed possum (*Trichosurus vulpecula*), European rabbits and hares (Family Leporidae), house mice and three rat species (Family Muridae). In addition, domestic livestock such as cattle and sheep (Family Bovidae) penetrate and damage native forests.

2 Critical aspects of candidate afforestation sites

2.1 Site factors

Site factors such as microclimate, water availability, legacy soil conditions, and accessibility for machinery are critical determinants of the design and success of any direct seeding operation. Sites available for native afforestation in New Zealand are typically on rugged, marginal, or remote land otherwise unprofitable for agriculture or commercial forestry, or which has been damaged by erosion or flooding. Afforestation with native species is also a desirable outcome following large-scale weed control operations, such as aerial herbicide application to control dense infestations of invasive northern hemisphere conifers, especially in inland South Island. Seeding with mechanical seed drills is of limited use for afforestation in these situations due to the difficult terrain and abundance of coarse woody debris. Aerially dispersed seed balls hold more promise for establishing native forest species into these types of sites (Griffiths et al. 2025).

2.2 Soil factors and root symbionts

Pastoral farming has significantly modified New Zealand's soil environment in the process of converting forested ecosystems to a grass (Poaceae) dominated landscape. As a result, the structure, chemistry and biology of soils in areas available for afforestation are far from what they would have been prior to deforestation. In particular, the availability of beneficial symbionts such as mycorrhizal fungi is very different in a pasture compared with a virgin native forest. Unlike other temperate regions, the majority of native trees in New Zealand form associations with arbuscular mycorrhizal fungi (AMF) (Orlovich and Cairney 2004). For example, kauri is associated with a high diversity of AMF taxa, as is the 'At Risk' myrtaceous tree *Lophomyrtus bullata* Burret (Padamsee et al. 2016; Ford et al. 2023). However, AMF communities can differ substantially between co-occurring native and non-native species in New Zealand (Ramana et al. 2023), so pastoral soil microbiomes may not be suitable for native AMF-dependent tree species (Horton et al. 2024).

Only members of the southern beech family, Nothofagaceae, are exclusively ecto-mycorrhizal (ECM), and two widespread pioneer tree species, mānuka (*Leptospermum scoparium* J.R.Forst. & G.Forst.) and kānuka (*Kunzea ericoides* (A.Rich.) Joy Thomps. *sensu lato*) both Myrtaceae, are able to form associations with both ECM and AMF (Teste et al. 2020). Molecular analyses of ECM associated with southern beech shows host specialization among the five native species (van Galen et al. 2023a), and limited overlap with ECM taxa found on introduced trees (Orlovich and Cairney 2004; Teasdale et al. 2012). Likewise, Kōwhai species (*Sophora*, Fabaceae) form associations with specific native nitrogen-fixing *Mesorhizobium* bacteria, rather than introduced *Rhizobium* strains associated with pastural legumes (Tan et al. 2015). This reliance on native soil symbionts creates additional issues when attempting to (re)establish native forest species on ex-agricultural land.

2.3 Competition from non-target plant species

Competition from existing vegetation, and weeds present in the soil seed bank, is one of the biggest obstacles to successful native afforestation in New Zealand, especially on ex-agricultural land (Ledgard et al. 2008). During the process of clearing New Zealand native forests for farming a vast array of pastoral grasses, forbs, and agricultural weeds were introduced and became naturalized in the landscape. When unmanaged, these species redirect natural successional processes and outcompete native seedlings (McQueen et al. 2006). In addition, woody weeds can be problematic when grazing pressure from feral or domestic stock is removed. For example, the woody leguminous shrubs gorse (*Ulex europaeus* L.) and broom (*Cytisus scoparius* (L.) Link) are widespread weeds of unmanaged agricultural lands especially in central and southern New Zealand and aggressively spreading naturalized northern hemisphere conifers affect c.1.7 million ha of agricultural and conservation land, mainly in eastern South Island (Wotton and McAlpine 2013).

3 Mitigating impacts for seeding

3.1 Site selection and preparation

An integral aspect of site preparation in New Zealand is the control of pre-existing herbaceous vegetation that could outcompete slower-growing natives. A common approach involves one or more applications of a broad spectrum herbicide. However, repeated broad spectrum herbicide treatments may have unintended negative consequences for soil microbiota (Helander et al. 2018). Non-herbicide methods such as scraping to remove the topsoil and the associated weed seed bank, followed by ripping to loosen the substrate, have been trialed at small scales in New Zealand and have potential value, as some native woody species establish well following soil disturbance (e.g., Allen et al. 1992; Ledgard et al. 2008). Plowing or ripping can be beneficial because it increases seed-soil contact and the extent to which seeds can imbibe water; these practices also alleviate soil compaction and help to eliminate resident vegetation (Ruthrof et al. 2013; Brown et al. 2023). The addition of woody debris may also aid in seedling establishment due to the creation of specialized microsites (Shemesh 2024).

3.2 Damage prevention

Successful forest restoration in New Zealand requires the removal or control of domestic livestock and feral browsers that damage native seedlings. For small to moderate sized projects this could involve fencing, but aerial or ground culling, as well as targeted poison operations such as rabbit control with Pindone [2-(2,2-dimethyl-1-oxopropyl)-1H-indene-1,3(2H)-dione], can provide adequate release from browsing pressure at large scales. Nurse crops can also aid native tree establishment by not only providing shelter but also restricting livestock access to seedlings. In a number of southern New Zealand studies, gorse has been shown to successfully shelter native trees establishing from seeds, eventually senescing as it is overtopped and shaded by the developing native canopy (Wotton and McAlpine 2013). Trials are also underway to investigate using areas of native bracken fern (*Pteridium esculentum* (G.Forst.)

Cockayne) to provide shelter and reduce browsing damage to native trees establishing from seed.

4 Seed procurement and preparation

4.1 Seed availability and eco-sourcing considerations

Lack of native seed supply is a significant impediment to seeding across New Zealand (Douglas et al. 2007). Natural seed sources and their associated genetic diversity have been depleted with the conversion of virgin forests into agricultural land over time (Norton et al. 2018). In addition, many native trees are bird (class Aves) pollinated and there is evidence that reductions in bird populations are affecting seed quantity and quality for some species (Anderson et al. 2020). The frequency of dioecy (separate male and female trees) and gynodioecy (separate female and hermaphrodite trees) is also unusually high among native New Zealand trees, meaning that effective population sizes are further reduced and only a limited number of trees can be relied on to provide high quality out-crossed seeds. Seed supply for afforestation in New Zealand is further complicated by the high frequency of masting among native trees including most of the southern conifer family Podocarpaceae, the southern beeches, and other key broadleaf species. These features of the native woody flora create particular challenges for seed collection and supply. However, the ability to predict heavy mast years from annual temperature differences of successive years (Samarth et al. 2020) now means seed collection efforts, e.g. positioning of nets under female trees, can be upscaled when seed is likely to be abundant. For tree species that reproduce annually, the seasonality of fruit maturation is fairly well known. For some species, fruit linger for some time on trees, e.g. many populations of the pioneer species mānuka exhibit serotiny, so capsules can be collected at any time of the year and heated to release the minute seeds. However, for fleshy-fruited trees, fruits are often rapidly removed by birds, so collection has to be well timed.

Due to the fragmented nature of the remaining natural forests, limited areas are available from which to collect locally appropriate, 'eco-sourced' seeds. Furthermore, there is evidence in New Zealand that small population sizes can lead to significant inbreeding depression in some tree species, meaning that local remnants may not produce any high-quality seeds (e.g., Robertson et al. 2011). Luckily, recent studies have demonstrated that there are low levels of regional genetic differentiation in many native trees, especially on South Island (Heenan et al. 2023), so seeds can legitimately be sourced from a wider area to maximize the genetic diversity of seeds being sown. Sourcing seeds from a wider area also allows practitioners to plan for climatic resilience via climate-adjusted provenancing (Prober et al. 2015), as forests established currently will very likely face challenging changes in rainfall and temperature regimes for decades to come.

4.2 Seed handling, cleaning and pre-treatment

Fleshy fruits are especially common among New Zealand native trees (Lord 1999) with the pulp containing germination inhibitors. Many species also have hard, thick seed coats. Standard seed pretreatments, including pulp removal, moist cold stratification, and scarification for hard coated seeds, have increased the ability to

efficiently germinate a range of New Zealand native tree species employed in afforestation (Metcalf 2007; Rowarth et al. 2007). Most fleshy-fruited species can be quickly cleaned in large quantities by floating them in water and agitating with a stab blender then pressing through a sieve. The germination of some species is also improved if flesh was left to rot off prior to sowing. Species with plumed or sticky seeds, such as *Pittosporum* Banks ex Gaertn. (Pittosporaceae) and *Olearia* Moench (Asteraceae) need to be treated before they are suitable for broadcasting or drilling. *Eucalyptus* L'Hér. oil has been successfully used as a pre-treatment to remove sticky residue from *Pittosporum* seeds (Table 1).

Research into the effects of chemical or hormonal treatments on germination rates of native species are still in their earlier stages, but there are some promising indications that gibberellic acid and potassium nitrate seed pre-treatments, can overcome seed dormancy for some species, and seed priming with sodium chloride and hydrogen peroxide can improve cumulative germination and germination rates for others (Moss-Mason 2024).

Table 1. Native New Zealand trees and shrubs used in direct seeding trials. Superscript 1: Overdyck et al. (2013); 2: Lord unpublished data (*Ngā Kāhano Whakahau* project); 3: estimates from Dodd and Power (2007); 4: Griffiths et al. (2025); 5: mean and maximum in short/long grass from Ledgard et al. (2008); 6: van Galen et al. (2022).

Species	Seeding method trialled	% Germination in field trials (FT) and/or viability tests (C)	Factors improving germination and establishment in the field
<i>Beilschmiedia tawa</i> (A.Cunn.) Benth. et Hook.f. ex Kirk	Seed balls ¹	FT 59%	Remove flesh, recalcitrant, sow fresh
<i>Coprosma propinqua</i> A.Cunn., Mingimingi (Rubiaceae)	Hand-Broadcast, Burford Tree Seeder, Cross-slot drill ²	FT <1%, C: >10%	Remove flesh, moist stratify, control weed and grass regrowth
<i>Coprosma robusta</i> Raoul, Karamu (Rubiaceae)	Hand-Broadcast ³ Seed balls ⁴	FT <5%, C >50%	Remove flesh, stratify in moist sand for 2 months
<i>Cordyline australis</i> (G.Forst.) Endl., Tī Kōuka (Asphodeliaceae)	Burford Tree Seeder ²	FT <1%, C >10%	Remove flesh, moist stratify, best in moister sites
	Hand-Broadcast ⁵	FT mean 5.4/8.3%, max 20/50%	
	Seed balls ⁴	C >90%	
<i>Corokia cotoneaster</i> Raoul, Korokia (Argophyllaceae)	Burford Tree Seeder, Cross-Slot drill ²	FT 0%, C 0%	Known to require after-ripening. Needs more work on seed biology
<i>Dacrydium dacrydioides</i> (A.Rich.) de Laub., Kahikatea (Podocarpaceae)	Enviromulch ²	FT 0%, C 0% likely seeds desiccated	Collect in heavy mast year, recalcitrant, AMF, more research needed
	Seed balls ⁴	FT 0%, C >10%	
<i>Entelea arborescens</i> R.Br. (Malvaceae)	Seed balls ⁴	C >50%	
<i>Fuscospora cliffortioides</i> (Hook.f.) Heenan et Smissen, Mountain Beech (Fagaceae)	Hand-broadcast ⁶	FT >10%, C >10%	Collect in heavy mast year, best sown fresh, shelter during establishment, control weed and grass regrowth, ECM
	Burford Tree Seeder ²	FT <1%, C <10%	
	Triple Disk drill ²	FT 0%, C <10%	
<i>Fuscospora solandri</i> (Hook.f.) Heenan et Smissen, Black Beech (Fagaceae)	Hand-broadcast, Burford Tree Seeder ²	FT <1%, C >10%	
	Cross-Slot drill ²	FT 0%, C >10%	
	Enviromulch ²	FT <10%, C >10%	

<i>Fuscospora truncata</i> (Colenso) Heenan et Smissen, Hard Beech (Fagaceae)	Seed balls ⁴	C <10%	
<i>Griselinia littoralis</i> Raoul, Kapuka (Griseliniaaceae)	Enviromulch ¹	FT <1%, C >10%	Remove flesh, sow fresh or moist stratify, recalcitrant, AMF
	Hand-Broadcast ³	FT mean 7.9/10.4%, max. 35/40%	
<i>Hoheria angustifolia</i> Raoul, Houhere (Malvaceae)	Burford Tree Seeder ¹	FT >10%, C >10%	Control weed and grass regrowth
<i>Kunzea ericoides</i> (A.Rich.) Joy Thomps., Kānuka (Myrtaceae)	Hand-broadcast, Burford Tree Seeder ¹	FT >10% C >50%	Control weed and grass regrowth, shade-intolerant, drought tolerant once established, thrives in gravel, AMF/ECM
<i>Leptospermum scoparium</i> J.R.Forst. & G.Forst., Mānuka (Myrtaceae)	Enviromulch, Hand-broadcast, Burford Tree Seeder ¹	FT >10%, C >10%	Control weed and grass regrowth, does not tolerate shade or drought, often seeds after fire, AMF/ECM
	Cross-slot drill ¹	FT <1%, C >10%	
	Seed balls ⁴	C >10%	
<i>Lophozona mensiezii</i> (Hook.f.) Heenan et Smissen, Silver Beech (Fagaceae)	Burford Tree Seeder, Cross-Slot drill ¹	FT 0%, C 0%	Collect in heavy mast year, sow fresh or moist stratify, ECM
	Seed balls ⁴	C >10%	
	Hand-Broadcast ⁵	FT mean 2.5/2.9%, max. 10/25%	
<i>Meliccytus ramiflorus</i> J.R. & G. Forster, Mahoe (Violaceae)	Hand-Broadcast ⁵	FT mean 4/0%, max. 5/0%	Remove flesh, stratify in moist sand for 2 months
<i>Myoporum laetum</i> G. Forst., Ngaio (Scrophulariaceae)	Hand-Broadcast ⁵	FT 0/0%	Remove flesh, stratify in moist sand for 2 months
<i>Myrsine australis</i> A.Rich, Red Mapou (Primulaceae)	Hand-Broadcast ⁵	FT >10%, C >50%	Control weed and grass regrowth, moist stratify, best in moist soils
<i>Phormium tenax</i> J.R.Forst. & G.Forst., Harakeke (Asparagaceae)	Enviromulch ²	FT: mean 6.7/2.1%, max. 25/10% ³	
<i>Pittosporum eugenioides</i> A.Cunn., Tarata (Pittosporaceae)	Hand-broadcast, Burford Tree Seeder, Cross-slot drill ²	FT 0%, C 0%	Remove sticky aril with <i>Eucalyptus</i> oil, control weeds and grass regrowth, delayed germination typical
<i>Pittosporum tenuifolium</i> Banks & Solander. ex Gaertn., Kohuhu (Pittosporaceae)	Hand-Broadcast ⁵	FT mean 12.9/16/7%, max. 60/50% in disturbed plots	
<i>Podocarpus totara</i> G.Benn. ex D.Don, Tōtara (Podocarpaceae)	Burford Tree Seeder ²	FT <1%, C >10%	Collect in heavy mast year, moist stratify, AMF
	Seed balls ⁴	C <10%	
<i>Pseudopanax arboreus</i> (L.f.) K.Koch, Five Finger (Araliaceae)	Enviromulch, Burford Tree Seeder ²	FT 0%, C 0%	Remove flesh, needs more work on seed biology
	Hand-Broadcast ⁵	FT mean 0/0.8%, max. 0/20%	
<i>Solanum aviculare</i> G.Forst., Poroporo (Solanaceae)	Hand-Broadcast ⁵	FT mean 10.4/2.5%, max. 45/15%	Remove flesh, stratify in moist sand for 2 months
<i>Sophora microphylla</i> Aiton, Kōwhai (Fabaceae)	Hand-broadcast, Burford Tree Seeder ²	FT >50%, C >90%	Scarify or nick. Seedlings vulnerable to rabbits, killed by clopyralid herbicides, <i>Mesorhizobium</i>
	Cross-slot drill ²	FT 0%, C >90%	
	Hand-Broadcast ⁵	FT mean 3.8/7.5%, max. 15/40%	

	Seed balls ²	C >90%	
<i>Veronica salicifolia</i> G.Forst., Koromiko (Plantaginaceae)	Burford Tree Seeder ²	FT >10%, C >50%	Control weed and grass regrowth, sensitive to clopyralid herbicides
	Cross-slot drill ²	FT 0%, C >50%	
	Seed balls ⁴	C >90%	
<i>Veronica stricta</i> Banks & Sol. ex Benth., Koromiko (Plantaginaceae)	Hand-broadcast ³	FT <1%, C >50%	

4.3 Seed storage

Knowledge gaps concerning native seed storage and germination requirements are apparent across many native tree taxa in New Zealand (Douglas et al. 2007; Metcalf 2007). It is thought that the majority of the flora produce orthodox seeds that can be stored for prolonged periods at reduced moisture content (Wyse et al. 2023). However, the seeds of some key native trees, including many native conifers, are recalcitrant, meaning they lose viability once dry and cannot be easily stored (Rowarth et al. 2007; Wyse et al. 2023). Detailed experimentation is needed for such species to determine optimal seed storage and germination conditions (e.g., van der Walt et al. 2020). Recalcitrance, combined with the fact that masting behavior is common among New Zealand trees (Webb and Kelly 1993) means that viable seed for some key tree species is only available in sporadic years and must be sown fresh for best effect.

5 Seeding methods in New Zealand

New Zealand has historically used aerial seeding to establish introduced conifers in remote hill country to combat accelerating erosion (Faulkner et al. 1972). However, seeding of native species is still the subject of research and development with very few large-scale projects implementing seeding for native afforestation. Douglas et al. (2007) reviewed the use of seeding for restoration in New Zealand and concluded that its applicability was constrained at that time by a lack of seed supply, knowledge of best-practice sowing times and rates, unreliable germination and seedling development, and competition from environmental weeds. For 10 years following the publication of that review only two seeding trials were attempted. Ledgard et al. (2008) trialed seeding into seven ex-pasture environments in Canterbury, New Zealand, using hand broadcasted seeds of 23 native tree and shrub species. They concluded that soil disturbance paired with herbicide application prior to seeding positively influenced the establishment of native species. At that time only one study on private land involving agricultural machinery had been conducted, which successfully established *L. scoparium* into plowed furrows (Ledgard et al. 2008).

5.1 Species composition and sowing density

Almost all trials to date have included a mix of nurse or pioneer species with late successional stage species in seed mixes. Nurse species have included agricultural crops such as annual oats (*Avena sativa* L.) and narrow-leaved plantain (*Plantago lanceolata* L.) that could provide some shelter for native tree seedlings but not compete with them. Native pioneer species have also been targeted in trials and proven to cope with most conditions. Sowing densities are conditional on application method but in most cases aim to ideally establish one surviving tree for every c. 2–3 m², i.e., a density of 3000–5000 stems ha⁻¹.

The inclusion in seed mixes of nurse species that germinate and grow rapidly to create a canopy is an effective means to control non-target species, particularly vigorous grass regrowth. Studies in southern New Zealand have successfully used the large bunchgrass toetoe (*Austroderia richardii* (Endl.) N.P.Barker et H.P.Linder, Poaceae), mānuka, kānuka, and koromiko (*Veronica* spp. L.) to rapidly create shade (Table 1). Many large-seeded, late successional tree species such as members of the Podocarpaceae and Lauraceae germinate slowly and over an extended period of time. Pioneer species can create conditions suitable for the emergence and survival of these slower-germinating, late successional trees species, which can either be introduced to the site along with fast growing pioneer species, or oversown at a later date once a preliminary woody canopy has formed. Seeding experiments by Paul et al. (2020) indicate that some experimentally sown large-seeded species can remain in the soil for more than a year and still emerge and establish. The inclusion of the dual mycorrhizal species mānuka and kānuka in seed mixes also provides potential hosts for ECM as well as AMF fungi, creating conditions that may facilitate the establishment of southern beech species (Nothofagaceae) which are obligately dependent on ECM fungi.

For species that require the formation of mycorrhizae for successful establishment, eco-sourced fungal spores or forest duff (litter layer, O, and uppermost A soil horizons) can be introduced along with seeds. For some New Zealand ECM fungi, spores from dried fungal fruiting bodies can remain viable and germinate after more than 120 days storage, providing a means of collecting and storing identified fungi for later use as inoculum (Bohorquez et al. 2019).

5.2 Sowing practices

Seeding via a range of methods has been the focus of a New Zealand government funded research project running from 2019–2024: *Ngā Kakano Whakahau: The Seeds Project*, led by the first author. This project aimed to test and refine seeding approaches for establishing native forest at scale on retired pasture in South Island, in conjunction with the delivery of beneficial mycorrhizal fungi to remediate soil microbiomes in deforested landscapes. Initial trials aimed to compare the cost vs. success of a range of seed application methods including hand broadcasting seeds, seed application within a mulch matrix, and direct drilling using a purpose-built tree seeder and agricultural seed drills. Some trials have already been published or made available as theses (e.g. Bohorquez et al. 2021; Van Galen et al. 2022; Barber-Sperling 2023; Strawsine et al. 2024; Horton et al. 2024). Additional results of the program are presented in the following sections.

5.2.1 Direct drilling

Advances in direct drilling for afforestation in Australia led to a consortium of interested parties importing an Australian invention, the Burford Tree Seeder, into New Zealand in 2016. Developed in South Australia by Rod Burford, the Burford Tree Seeder has been used for restoration in Australian shrub and grasslands, with generally high success (Streatfield 2019). The Burford has a single disc coulter that scalps a furrow of varying width, then seeds are deposited at a specified depth within the furrow via a single tine. Seed size determines the ideal seeding depth; larger seeds benefit from

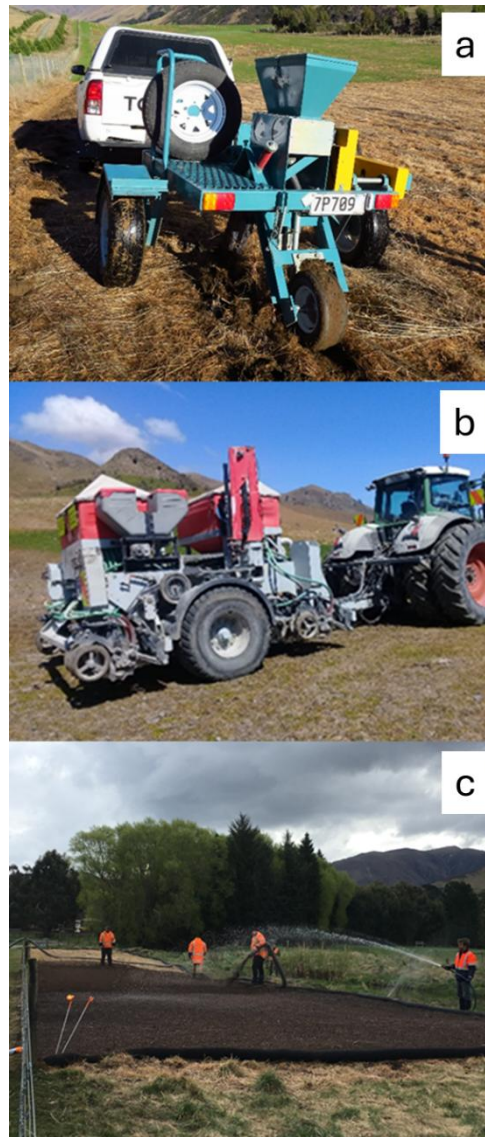


Figure 2. (a) Burford Tree Seeder being towed by a 4-wheel-drive vehicle; (b) Cross-Slot™ agricultural drill towed by a tractor; (c) Enviroblanket™ Mulch application (Photo credits: Janice Lord).

burial no deeper than two times the size, whereas smaller seeds are better suited to placement on top of the soil surface (Bewley and Black 1994). Two separate seed hoppers on the Burford can deliver small and large seeds independently, so that while large seeds are sowed at depth by the tine, small seeds can be deposited on the surface of the furrow base and pressed into the ground with the press wheel. Also, as tillage, in the form of scalping a furrow, coincides with seed drilling, no prior cultivation is required, however, considerable site preparation in the form of repeated herbicide applications is recommended to reduce competition from weeds (Streatfield 2019). The Burford most effectively drills on bare land with no thatch or rocks and can only be used where 4-wheel-drive (4WD) vehicle access is safe, making it inappropriate for hilly, wet, or stony landscapes (Figure 2). However, the size of the Burford makes it easily transportable between sites. In recent years, multiple trials with the Burford Tree

Seeder, facilitated by the New Zealand Department of Conservation and more recently the commercial enterprise SeedNZNatives (<https://www.seedznatives.co.nz>), have been established in southern and eastern South Island (e.g., Figure 3). Best results from seed drilling trials in southern New Zealand using the Burford Tree Seeder have been for areas sown in spring on ex-agricultural sites that had been prepared with two herbicide applications in the previous spring and autumn. In areas with milder winters, autumn establishment can provide seeds with natural moist stratification conditions. All sites also had two follow-up selective herbicide applications to control weed regrowth (Streatfield 2019).

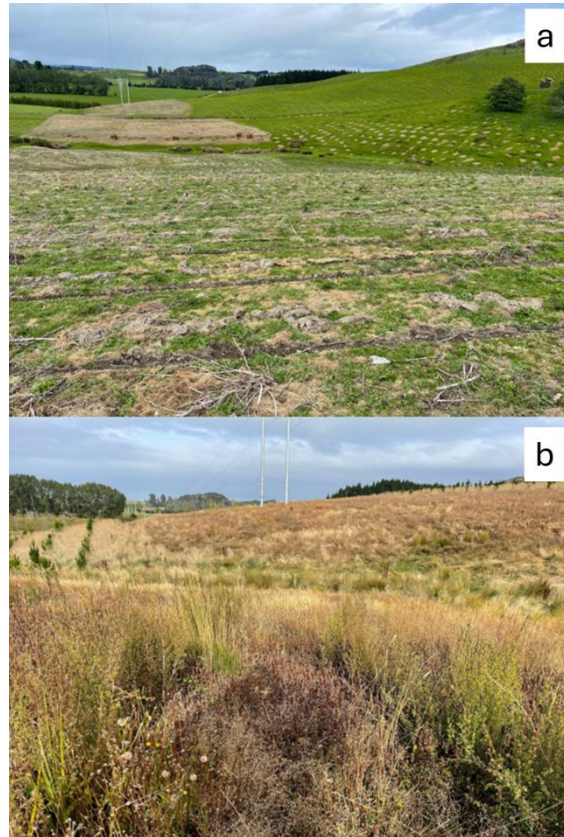


Figure 3. Native tree corridor sown under power lines with Burford Tree Seeder between areas planted with *Pinus radiata* D.Don, Table Hill, Otago. (a) Immediately after sowing, 29 October 2021; (b) 17 month old mānuka (*Leptospermum scoparium* J.R.Forst. & G.Forst.) and tī kouka (*Cordyline australis* (G.Forst.) Endl.) indicated, 29 March 2023 (Photo credits: Pieter Britz, Seed NZ Natives Ltd.).

As part of The Seeds Project, the Burford Tree Seeder was compared with two conventional agricultural drills – the Cross-Slot™, a no-till precision drill developed in New Zealand (Figure 2), and a standard triple disk drill (Lord, unpublished data). The same native seed mix was sown using the Burford Tree Seeder and the Cross-slot drill on 2 ha of retired cropping and pasture in inland Canterbury, South Island. The 4WD vehicle towing the Burford Tree Seeder was unable to navigate the rocky sloped areas accessible to the tractor towing the Cross-Slot drill, so some differences between sown areas were unavoidable. The standard triple-disk drill was trialed at a separate site in inland Otago, South Island, with a less species diverse seed mix. Both the Cross-slot drill

and Burford Tree Seeder were capable of delivering small amounts of seeds over the study area. However, the triple disc drill required a minimum of 15–20 kg of seed to be operational regardless of the size of area to be drilled. In that trial we used 4 kg of native tree seed supplemented by 16 kg of annual oats, which was an economic solution to the issue of seed volume. Inviolate granular material such as processed rice (*Oryza sativa* L.) or sand (e.g., Otago South Rivercare 2024) could also be effective at adding volume to native seed mixes without introducing additional species that might compete with native species.

We had expected that the no-till Cross-Slot might result in lower weed regrowth as it does not turn a furrow, instead it deposits seeds to a precise depth within an inverted T-shaped slot cut directly into the soil and closed over with a press wheel. However, weed regrowth did not differ significantly between drill types. Seedling emergence and survival was higher in the Burford Tree Seeder area than in the areas sown with the agricultural drills, likely because the variability in deposition depth, and also the creation of a heterogeneous germination tilth in the furrow provided a greater variety of microsites that would suit a mixture of species.

5.2.2 Pneumatic seeding within a mulch matrix

The EnviroBlanket™ Mulch seeding method, developed and implemented by RedTree Environmental solutions (<https://redtree.co.nz/>) consists of a custom blended mulch applied aurally or under pressure together with a site-specific mixture of native seeds (Figure 2). As part of The Seeds Project in inland Canterbury, Enviroblanket trials were applied along a riparian strip unsuitable for vehicle access (Lord, unpublished data). The site was prepared with two applications of broad spectrum herbicide several months before trial establishment. A thick layer of mulch was first deposited on the site as a weed suppressant, then a thin layer of mulch and seeds added. Trials were initially watered to help compact the mulch but not watered thereafter. Some seedlings of pioneer species emerged from the EnviroBlanket mulch, but none survived beyond the first year. The reasons for this were most likely that weeds were not adequately controlled prior to establishment or during the trial, and the species sown were not able to tolerate the severe site conditions over the ensuing 18 months—a very dry summer, followed by a very cold winter. While this method has proven useful for revegetating difficult access sites lacking in germination microsites (e.g., exposed rocky slopes), it was not cost effective for large-scale afforestation on retired agricultural soils with a large residual weed seed bank.

5.2.3 Aerial seeding

Aerial seeding using a mixture of seeds and ballast such as sand or rice, or using seeds encapsulated into balls, allows desirable species to be introduced into otherwise inaccessible areas, or into disturbed sites after events such as wildfires and landslips cost-effectively (Xiao et al. 2015; Griffith et al. 2025). Seeding native species aurally has been receiving increasing attention in New Zealand. In 2022, the Otago South Rivercare group trialed aerial seeding combined with stock trampling and follow-up weed control with aurally applied herbicide. Two years after the trial, a range of herbicide tolerant species had successfully established, and additional trials are ongoing (Otago South Rivercare 2024). Aerial seeding has also been the focus of a recent project funded by the New Zealand Ministry for the Environment involving the authors, the New Zealand

Department of Conservation, and the commercial drone company Envico Technologies (<https://www.envicotech.co.nz/>). Pioneer species such as mānuka, kānuka, koromiko, and toetoe, as well as the monocotyledonous tree tī kōuka (*Cordyline australis* (G.Forst.) Endl., Asparagaceae) and the broadleaved trees kōtukutuku (*Fuchsia excorticata* (Forst. & Forst. f.) L. f., Onagraceae) and poroporo (*Solanum aviculare* G.Forst., Solanaceae) show promise for large-scale dispersal via seed balls. Formulation, viability, and dormancy issues still require more work for larger-seeded and/or late successional tree species to be established via this method (Griffiths et al. 2025; Lord et al. 2025).

6 Post-sowing practices and maintenance

While initial shelter seems to improve seedling survival, post-emergence weed control is critical to establishment, especially control of the vigorous regrowth of introduced pasture grasses and clovers (*Trifolium* spp. L.) in ex-agricultural sites. Targeted herbicides such as haloxyfop-P and clopyralid have proven particularly effective for controlling competition from grasses and clovers (van Galen et al. 2022), but obviously these would have negative impacts on sensitive native grasses and legumes. Furthermore, the long-term impacts of herbicide use on native plants and soil microbiota is still unknown. Due to the damage that introduced herbivores such as hares, rabbits, deer, and Australian brush-tailed possums inflict on the regeneration of native species, an integrated pest control plan involving fencing, trapping, shooting, and or poisoning needs to be included as a central focus of seeding operations (Forbes et al. 2020).

7 Factors affecting success and failure

Fast germinating pioneer species are more amenable to seeding efforts, due to their ability to establish rapidly in fluctuating field conditions (e.g., Figure 3). Woody pioneer species currently known to be suitable for establishment from seed at large scales in temperate New Zealand include mānuka, kānuka, *Hoheria* spp. A.Cunn., *Plagianthus* spp. J.R.Forst. & G.Forst., whau (*Entelea arborescens* R.Br.) (three Malvaceae trees), and koromiko, due to seed availability, viability, and ease of handling. However, small-seeded species such as mānuka and kānuka, which naturally germinate after soil disturbance, appear less able to tolerate competition from resident vegetation, especially from dense mats of introduced pasture grasses and clovers, so post-establishment weed control is imperative. Among larger-seeded or late successional tree species, seeding trials in southern New Zealand (e.g., Ledgard et al. 2008; Streatfield 2019; Paul et al. 2020; Barber-Sperling 2023; van Galen et al. 2024) have had some success with freshly collected, as well as moist stratified, mountain beech (*Fuscospora cliffortioides* (Hook.f.) Heenan et Smissen), cleaned and stratified tī kōuka, *Coprosma* J.R.Forst. & G.Forst. (Rubiaceae), *Pittosporum* spp., and scarified kōwhai (*Sophora* spp. L., Fabaceae) (Table 1). More research is needed on other large-seeded native New Zealand species. Potential also exists to transition non-native forests to native forests using the non-native canopy as a nurse crop to suppress competing vegetation, as many native woody species can establish under non-native canopies (Pritchard et al. 2024).

Success is also dependent on the availability of high-quality seed, which is limited to mast years for many species. Fresh mountain beech seed produced in a heavy mast year germinates readily when hand seeded into retired pasture. Shelter in the

form of long grass or bracken slash is critically important to early-stage survival of beech seedlings, but release from grass competition benefits establishment (van Galen et al. 2022). Mountain beech seeds can be stored dry, vacuum-packed, and frozen at -20 °C for some years, then primed for germination via soaking and wet stratification to restore germinability (van Galen et al. 2023b). Similar storage and germination trials need to be conducted for other key native tree species, but especially other mast seeding species to ensure a continuous supply of seeds. Mast seeding species with recalcitrant seeds, such as kahikatea (*Dacrycarpus dacrydioides* (A.Rich.) de Laub.) and rimu (*Dacrydium cupressinum* Sol. ex Lamb.), both in the southern conifer family Podocarpaceae, are especially problematic, with success dependent on using fresh seed promptly when it is available in large quantities.

The availability of appropriate soil symbionts such as mycorrhizal fungi is another component of success when seeding. In a hand-seeding trial with mountain beech, final seedling height was correlated with mycorrhizal abundance on roots (van Galen et al. 2022). Furthermore, the ability of mānuka to survive drought in another study was related to the availability of appropriate mycorrhizal inoculum (Strawsine et al. 2024). Some native trees associated with AMF fail to establish in the absence of appropriate inoculum, including conifers such as tōtara (*Podocarpus totara* G.Benn. ex D.Don, Podocarpaceae), as well as broadleaved trees, e.g. Kapuka (*Griselinia littoralis* Raoul, Griselinaceae) (Baylis 1959; Williams et al. 2012).

Failure of seeding trials in New Zealand generally arises from poor site selection or germination, leading to low seedling survival. Seeds of many native tree species do not germinate rapidly even under optimal conditions, which places these species at a severe disadvantage in a field situation where rapid establishment before weed regrowth is desirable. Research is needed into seed priming of native species for optimal germination rates (Moss Mason 2024).

Site conditions have also been a major barrier to seeding success in New Zealand. While New Zealand has a temperate climate, some regions experience significant drought that is thought to be one of the biggest obstacles to direct drilling success nationally, especially for a flora that is not considered especially drought adapted (Douglas et al. 2007). Selection of sites with predictable rainfall, particularly in autumn and spring will likely increase the success of direct drilling for afforestation in New Zealand (Douglas et al. 2007; Streatfield 2019). The seed drilling trials mentioned in this review were mainly in areas of retired pasture, which suffered from substantial grass regrowth that often out competed slow growing native seedlings. A strict regime of repeated pre- and post-establishment herbicide applications are needed to reduce competition from weeds. Scraping away topsoil and the associated weed seed bank, and ripping to create germination microsites, are also promising avenues for further work. Seeding into relatively weed free environments after large scale weed control, such as aerial application of herbicides to invasive conifers, is another promising avenue for further research. Seeding after natural disasters (e.g., cyclones or wildfires) could also be investigated as a means for native seedlings to establish without, or with reduced, weed competition, even though wildfires were not a natural disturbance in pre-human New Zealand forests.

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This paper may include research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All use of pesticides must be registered by appropriate agencies before they can be recommended.

CAUTION

Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or wildlife if they are not handled or applied properly. Use all herbicides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and their containers.

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