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Biomass and root attributes of eight of New Zealand's most common indigenous evergreen conifer and broadleaved forest species during the first 5 years of establishment

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Abstract

Background: Tree allometric equations are critical tools for determining tree volume, biomass and carbon stocks. However, there is a lack of species-specific biomass equations for juvenile trees of many of New Zealand's indigenous species. The aim of this study was to provide allometric equations for total above- and below-ground biomass and total root biomass and length for eight common evergreen conifer and broadleaved species.

Methods: In a plot-based field trial, growth metrics of conifers *Prumnopitys taxifolia* (matai), *Agathis australis* (kauri), *Prumnopitys ferruginea* (miro), *Podocarpus totara* (totara), *Dacrycarpus dacrydioides* (kahikatea) and *Dacrydium cupressinum* (rimu) and broadleaved species *Alectryon excelsus* (titoki) and *Vitex lucens* (puriri) were measured annually. These species were selected based on their potential role as a long-term solution for mitigating erosion in areas of marginal land proposed for new afforestation/reforestation and as an important carbon (C) sink.

Results: Root collar diameter (RCD) provided the best fit for tree height, total above-ground biomass (AGB) and total below-ground biomass (BGB), and all regressions were highly significant ($P = 0.001$). Most species showed significant increases in annual growth and, by year 5, the BGB ranged between 21 and 42% of total biomass and decreased with increasing plant age. Of the conifers, *Podocarpus totara* had the greatest mean maximum root spread (2.2 m) exceeded only by the broadleaved *Vitex lucens* (2.5 m). For all species, and in each year of the trial, 100% of the BGB remained confined to within 0.5 m of the ground surface. With the exception of *Vitex lucens* and *Podocarpus totara*, > 90% of the total root length remained within a 0.5-m radius of the root bole. The species-specific mean tree biomass of 5-year-old plants ranged from 0.32 to 4.28 kg plant⁻¹. A mixed-species forest established at 1000 stems per hectare (spha), consisting of 200 of each of the best performed of the trialled species, would amass ~2.3 t ha⁻¹ of biomass and a forest carbon stock of 3.8 t CO₂ ha⁻¹ within 5 years.

Conclusions: Inter-species differences in the allocation of BGB and AGB appeared to be age dependent. The root-growth metrics of these common indigenous forest species, as candidates for erosion control, have improved our understanding of their potential usefulness for stabilising marginal land. Whole-plant biomass of juvenile trees will greatly improve the accuracy of current estimates of forest carbon stocks for proposed new areas of indigenous afforestation/reforestation.

Keywords: Biomass, Root systems, Conifer and broadleaved species, 5-year plot-based trial

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Background

Before human settlement, New Zealand was almost completely vegetated with indigenous evergreen podocarp (mainly conifer) and broadleaved forest in the lowlands (~200 m), transitioning to *Nothofagus* forest at elevations above 600 m to the tree line at 1050 m and alpine-subalpine shrubland and grasslands on the highest parts of the axial ranges (McGlone 1988; Wilmshurst 1997). However, since Maori (beginning ~600 years BP) and then European settlement (starting in the 1820s), much of New Zealand's indigenous forest has been cleared for conversion to pastoral use, for the development of a forest industry involving non-indigenous species and/or for urban development. By the time the first National Forest Survey began in 1945, only 25% of indigenous forest remained on a total land area of 26.6 million hectares, mostly in mountainous (difficult to farm) areas (Masters et al. 1957). In more recent years, the ongoing clearance of vegetation has led to the progressive loss of biodiversity and degradation of waterways and water quality through increased erosion, sedimentation and nutrient pollution.

An increase in awareness of the poor health of New Zealand's remaining areas of indigenous forest (as well as public and government pressure to maintain and enhance the indigenous biodiversity of New Zealand) (Parliamentary Commissioner for the Environment 2002) has encouraged reversion of cleared land back to forests. The planting of indigenous trees has become an integral part of indigenous-forest restoration efforts. Furthermore, since ratifying the Kyoto Protocol (Intergovernmental Panel on Climate Change (IPCC) 2000; New Zealand Climate Change Office 2003), New Zealand proposed to reduce its carbon emission target in the short to medium term through afforestation/reforestation. Exotic forests established on former grasslands since 1990 are likely to provide the major carbon offsets, but it has been recognised that an important additional carbon sink could be created through afforestation/reforestation of steep, erosion-prone pastoral hill country that environmentally is marginal for long-term agriculture by using indigenous shrubs and trees (Tate et al. 2000; Tate et al. 2003, Trotter et al. 2005). Relatively little is known about carbon sequestration by indigenous shrub species, but the density and diversity of species typical of naturally reverting stands suggests that relatively high levels of carbon storage are achievable. A range of additional objectives in sustainable environmental management will also be achievable. These include improving indigenous biodiversity, erosion mitigation and soil conservation and consequent improvements in water quality. Importantly, from a carbon-sink perspective, indigenous shrubs provide the first step to a successional pathway to a permanent cover of indigenous tall forest (Hall 2001;

Wardle 2002). The resultant forests typically comprise long-lived conifers and broadleaved species that can achieve large stature and an active growth phase that extends from 150 to 500 years (Hall 2001, Hinds and Reid 1957). As suggested by Hasselmann (1997), active net carbon accumulation over such time frames is consistent with the prolonged effort likely required to effect significant reductions in atmospheric carbon dioxide (CO₂) levels.

Given the pressing need to quantify carbon fluxes associated with terrestrial vegetation dynamics, an increasing number of researchers have sought to improve estimates of tree volume, biomass and carbon stocks. Many New Zealand-based studies have attempted to quantify the biomass of indigenous forest stands, mainly for live-tree carbon sequestration (Carswell et al. 2012; Scott et al. 2000; Trotter et al. 2005; Beets et al. 2014; Schwendenmann and Mitchell 2014; Dale 2013¹). These use allometric functions based largely on figures derived for individual specimens of a single species such as kānuka (*Kunzea ericoides* var. *ericoides* (A. Rich.) J. Thompson), and, where available, published values for a limited number of other species (Russo et al. 2010). The few available biomass relationships are for a handful of old-growth indigenous tree species from a subset of New Zealand forest classes and from a limited number of sites (Beets 1980; Allen et al. 1998³; Peltzer and Payton 2006⁴; Beets et al. 2008²). Thus, where species-specific and/or regional values remain unavailable, congeneric values have been used instead or in their absence, the mean of all published values (Beets et al. 2008). Furthermore, the majority of these studies were of mature trees though the age of the sample trees was not always determined.

Tree allometric equations are critical tools for determining tree volume, biomass and carbon stocks and have the potential to improve our understanding about carbon sequestration in woody vegetation to support the implementation of policies and mechanisms designed to mitigate climate change (Jara et al. 2014). In New Zealand, substantial gains have been made in improving the accuracy of the above-ground live tree carbon stored in the most widely distributed forest and shrubland ecosystems following the establishment of a nationwide network of permanent sample plots, (Carswell et al. 2012; Scott et al. 2000; Trotter et al. 2005; Peltzer and Payton 2006; Beets et al. 2014). Nonetheless, as identified by Peltzer and Payton (2006), there remains a growing need for further age-specific and species-specific allometric relationships particularly for the 20 most abundant species that comprise 90% of the total live-tree carbon in old-growth forests. However, the below-ground biomass component has proven difficult to quantify for old-growth trees. In particular, little is known about root allocation

except that there are interspecies differences in root distribution. Each species is known to allocate differing proportions of their total biomass to roots at different stages of growth, but overall, species-specific allocations of dry matter to roots are generally poorly documented (Korner 1998). Other than destructive sampling, there are few techniques with which to assess either the below-ground biomass component or the architectural differences in root system attributes between species. The use of non-invasive techniques such as ground-penetrating radar (GPR) is limited to coarse-root systems (Hruska et al. 1999). The fine-root components are particularly difficult and expensive to measure accurately. Several New Zealand and international studies have shown that roots comprise approximately 20% of the above-ground live tree biomass (Watson and Tomblason 2002; Beets et al. 2007). The precision of these root estimates, however, tend to be low (Hall et al. 2001) but have nonetheless been used in the absence of better species- and age-specific data. Furthermore, studies that have attempted to extract the majority of the below-ground root biomass often exclude the stump (Will 1966; Heth and Donald 1978; Watson and O'Loughlin 1990) and therefore underestimate the below-ground to above-ground biomass ratio. Previous authors (e.g. Cairns et al. 1997; Coomes et al. 2002) have suggested a value of 20% can be applied generally, but more work is needed before this figure can be accepted internationally.

Nationally, about 1.45 million hectares (Mha) of marginal pastoral land are suitable for afforestation/reforestation by indigenous shrubs or forests (Trotter et al. 2005). The enactment of the Permanent Forest Sink Initiative (PFSI) and Afforestation Grant Schemes (AGS) in 2008 and 2015, respectively (Ministry for Primary Industries 2015), and the introduction of forestry to the Emissions Trading Scheme (ETS) have strongly incentivised the planting in new areas of indigenous shrublands and/or successional tall forest species as a means of further reducing greenhouse gas emissions and ensuring that New Zealand meets both its short- and long-term obligations under the Framework Convention for Climate Change (FCCC). Given the current interest in the retirement of economically and environmentally unsustainable pastoral steep lands, the planting of successional indigenous forest species with a longer rotation and higher wood value may become an alternative and viable land use option for these areas. Furthermore, a species change to indigenous shrubs and/or forest trees could potentially alleviate issues currently associated with harvesting non-native species (predominantly *Pinus radiata* D. Don) that were originally established for erosion control, particularly in terrain with a high risk of storm-induced landslides. Issues include excessive amounts of sediment and associated woody debris,

damage to infrastructure and the degradation of stream habitats. However, more fundamental knowledge is required on the differences in relative growth rates between indigenous shrubland, conifer and broadleaved species and more specifically on the contribution of their root systems towards shallow soil reinforcement, especially during their formative years. Such data will assist in evaluating the potential effectiveness of various species both as plantings on marginal land degraded by erosion and as a longer-term land-use option for areas retired from exotic forest production. As is the case for old-growth indigenous forests, such data for the early-growth period of the majority of indigenous shrub and forest species have not been collected to date. Such data are essential for the development of allometric relationships for measuring the live-tree carbon sequestration for: (i) planted areas of juvenile shrubs and mixed species of indigenous conifer and broadleaved forests; (ii) areas of abandoned pasture currently in the juvenile stage of reverting to shrubland; and (iii) areas of exotic forest with 'high environmental risk' and likely to be converted (planted or by natural reversion) to a longer-term, and more sustainable, mix of indigenous shrubland and conifer/broadleaved forest.

This study is the first known attempt to systematically quantify, as a time series, both the above- and below-ground growth metrics for eight of New Zealand's most common indigenous conifer and broadleaved forest species during their early growth period (years 1 to 5). The goals of this study were to: (i) develop species-specific allometric equations to better estimate above- and below-ground live-plant biomass/carbon storage for areas of newly planted marginal land established as a pathway to a permanent indigenous forest and long-term carbon sink; and (ii) provide the first-ever description and classification of their root morphology and architecture and measurements of their root metrics (biomass, length and the spatial distribution of roots with increasing distance from and below the root bole). Such data form the basis for assessing their potential effectiveness as an alternative land-use option in areas degraded by erosion and deemed marginally sustainable for pastoralism and/or for areas currently unsustainable as short-term rotation exotic forest.

This paper does not address: (i) the effect of containerised versus bare-rooted seedlings on plant growth; nor (ii) the impacts of the wider range of ecological and environmental stresses known to influence plant development (e.g. competition for nutrients and water, soil texture and fertility; water-logging; drought; elevation; climate regime; exposure to wind and sun; shade; and grass suppression) since it is a site-specific study; nor (iii) silviculture and management practices other than planting density requirements needed to achieve effective

mitigation of erosion. Information on ecological and site requirements and growth parameters of mature trees of the selected species are provided in Additional file 1 and has been sourced from previous research by Foweraker (1929), McSweeney (1982), Pollock (1986), Salmon (1986), Poole and Adams (1994) and Wardle (2002). The ecology, establishment, growth and management of the studied species for wood production is adequately discussed by Bergin (2003), Bergin and Steward (2004), Bergin and Gea (2005, 2007) and Steward and Beveridge (2010).

Methods

Study site

The trial site was located on a low-lying, even-surfaced alluvial terrace adjacent to the Taraheru River, in Gisborne City (Fig. 1). The same site has also been used to measure 'plant growth performance' of: (i) 12 early (colonising) indigenous species considered typical of riparian margins (Marden et al. 2005); (ii) different clones of poplar and willow (Phillips et al. 2014); and (iii) a range of exotic forest species (Phillips et al. 2015). Temperatures over summer average 23 °C and over winter 12 °C, and mean annual rainfall is 1000 mm. The soil is a naturally fertile, free-draining Typic Sandy Brown Soil of the Te Hapara soil series (Hewitt 2010). Although not used, a drip-irrigation was installed to ensure survival of the plants in the event that drought could jeopardise the longer-term aims of this trial.

The soil has no physical or chemical impediments to root development to about 1.2 m depth, other than a variable-depth water table that fluctuates between > 1.5 m depth and within ~0.2 m of the surface (Phillips et al. 2014).

Trial design

The site (50 × 20 m) was tilled, and weed mat was laid down before planting in autumn 2006 (Fig. 1). Weed mat reduced weed competition and minimised efforts to extricate intertwined roots belonging to weeds from the anticipated dense and fibrous root network of the trialled species.

Containerised seedlings sourced from a local nursery consisted of 1.2-L polythene bags (0.12 m deep by 0.10 m diameter) filled with a 50:50 mix of bark and pumice. To minimise root disturbance, seedlings were planted with the soil attached. Root binding was minimal and root pruning before planting was not required as tap root length did not exceed the depth of the planting bag. The site was subdivided into three blocks and all three blocks were planted in 1 day. A randomised block design was used with equal numbers of each species in each block. Trees within blocks 1 and 2 (plants to be extracted 1 and 2 years after planting, i.e. at age 3 and 4 years old, respectively) were planted at 1-m spacing,

and in block three (plants to be extracted 3 years after planting, i.e. at age 5) at 1.5–2.0-m spacing to allow for increases in canopy and root growth during the course of the trial.

Species selection

The species chosen (Table 1) include those that succeed early colonising species to become a significant component of areas of mature coniferous/broadleaf forests found in most regions throughout the North Island of New Zealand (Allan Herbarium 2000). The conifers (softwoods) selected included rimu (*Dacrydium cupressinum* (Lambert)), totara (*Podocarpus totara* (D. Don)), miro (*Prumnopitys ferruginea* (D. Don) Laubenf.) and kahikatea (*Dacrycarpus dacrydioides* (A. Rich.) Laubenf.) because they are among the most abundant species that collectively contribute 90% of New Zealand's total live-plant carbon by volume (Peltzer and Payton 2006). Together with matai (*Prumnopitys taxifolia* (D. Don) Laubenf.), kauri (*Agathis australis* (D. Don) Lindley) and the broadleaved species titoki (*Alectryon excelsus* (Gaertner)) and puriri (*Vitex lucens* (Kirk)), these are among the most common species planted in landscape restoration projects (Bergin and Gea 2005, 2007). These species are considered as potential alternatives to the non-native species currently used in commercial planted forests to meet a range of economic, erosion-mitigation and other environmental benefits. Advantages include: tolerance to a wide range of climate, soil and topographic site conditions; seedlings are widely available; and their longer growing cycles are considered to be more sustainable than faster-growing non-native species.

Data collection

A group of 1- and 2-year-old plants were removed from their containers and destructively partitioned into their component parts. At the trial site, another group of 2-year-old seedlings were planted and a subset of plants was excavated and similarly destructively partitioned on the anniversary of planting for three successive years. An air lance at 240 kPa was used to remove the soil surrounding each root system without damage or significant loss of the fine root mass. The aim was to sample ten plants per species per year, but frost killed some puriri plants and stem breakage reduced the sample size of titoki plants (Table 1).

Tree height, canopy spread, root collar diameter (RCD—measured overbark at ground level) and diameter at breast height (DBH—measured at 1.4 m above-ground level) (where applicable) were measured before removing the plants from the trial site (Additional file 2). Canopy spread was taken as the mean of the diameter measured in two directions at right angles. Trees were

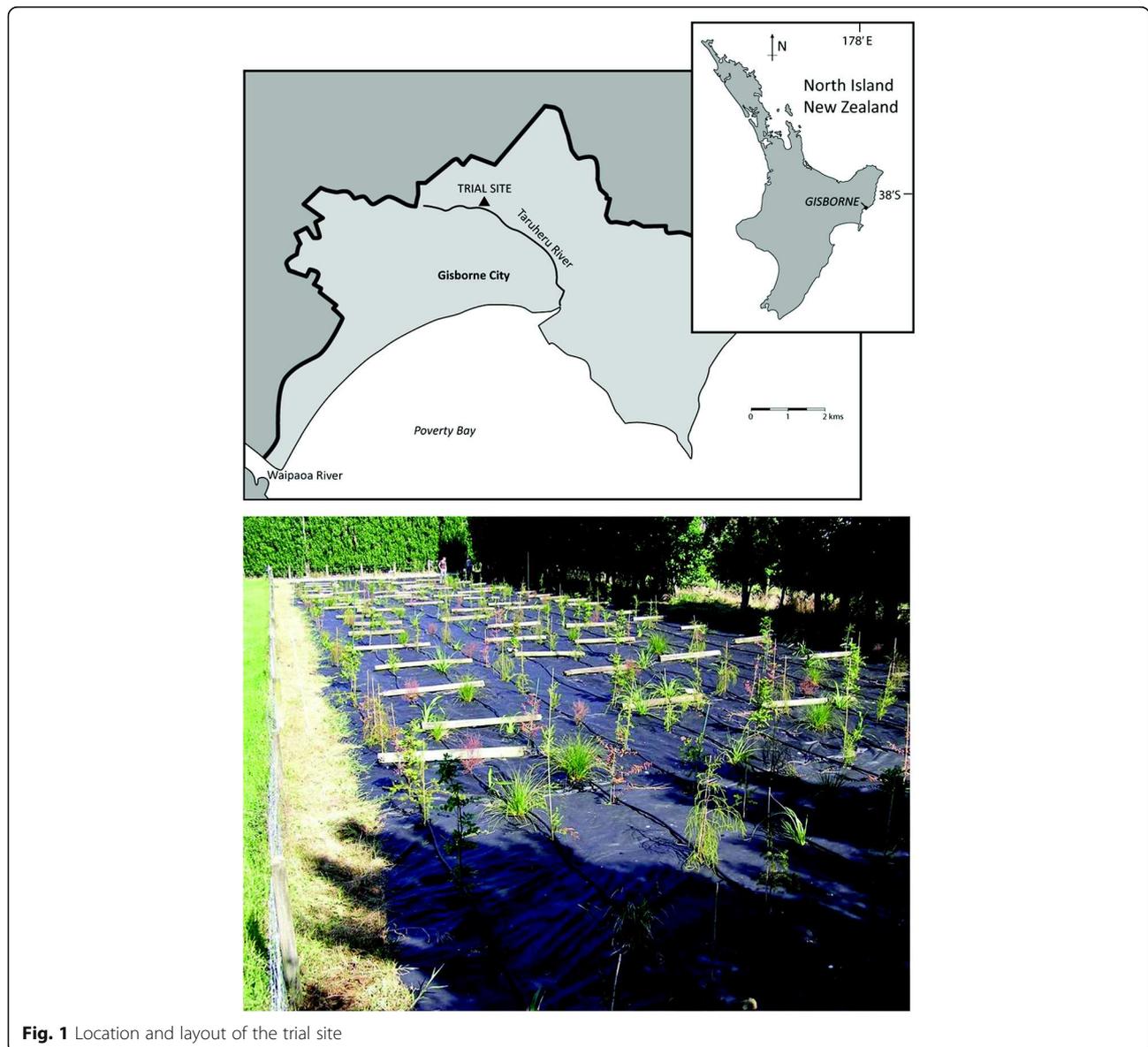


Fig. 1 Location and layout of the trial site

cut at ground level and the above-ground components separated into branches, foliage and stem (Additional file 3). Root system extraction and measurement methods followed well-established procedures (e.g. Watson et al. 1999; Marden et al. 2005; Phillips et al. 2014, 2015). Once removed from the ground, the root system of each plant was washed to remove adhering soil matter then photographed (an example is shown in Fig. 2). It was then described using the classification of Hinds and Reid (1957) before being partitioned into root bole (stump) and roots. Below-ground growth parameters included mean root depth and mean root spread of the lateral roots, hereafter referred to as root depth and root spread (Additional file 4). The latter was taken as the mean

of the maximum root length measured from root tip to root tip in two directions at right angles to each other. Root length (excluding fibrous roots) within each of the root diameter size classes was measured by laying pieces of root end for end alongside a tape measure (Watson et al. 1999). The mass of the roots and root bole were calculated separately (Additional file 5). Root distribution by mass (Additional file 6) and length (Additional file 7) relative to the root bole was obtained by systematically dissecting the root systems into 0.5-m radial and depth segments then sorted by diameter size classes, (< 1 mm fibrous, 1–2, 2.1–5.0, 5.1–10.0 and 10.1–20.0 mm over bark) (Watson and O’Loughlin 1990).

All plant components, both above- and below-ground, were oven-dried at 80 °C for 24 h or until no further

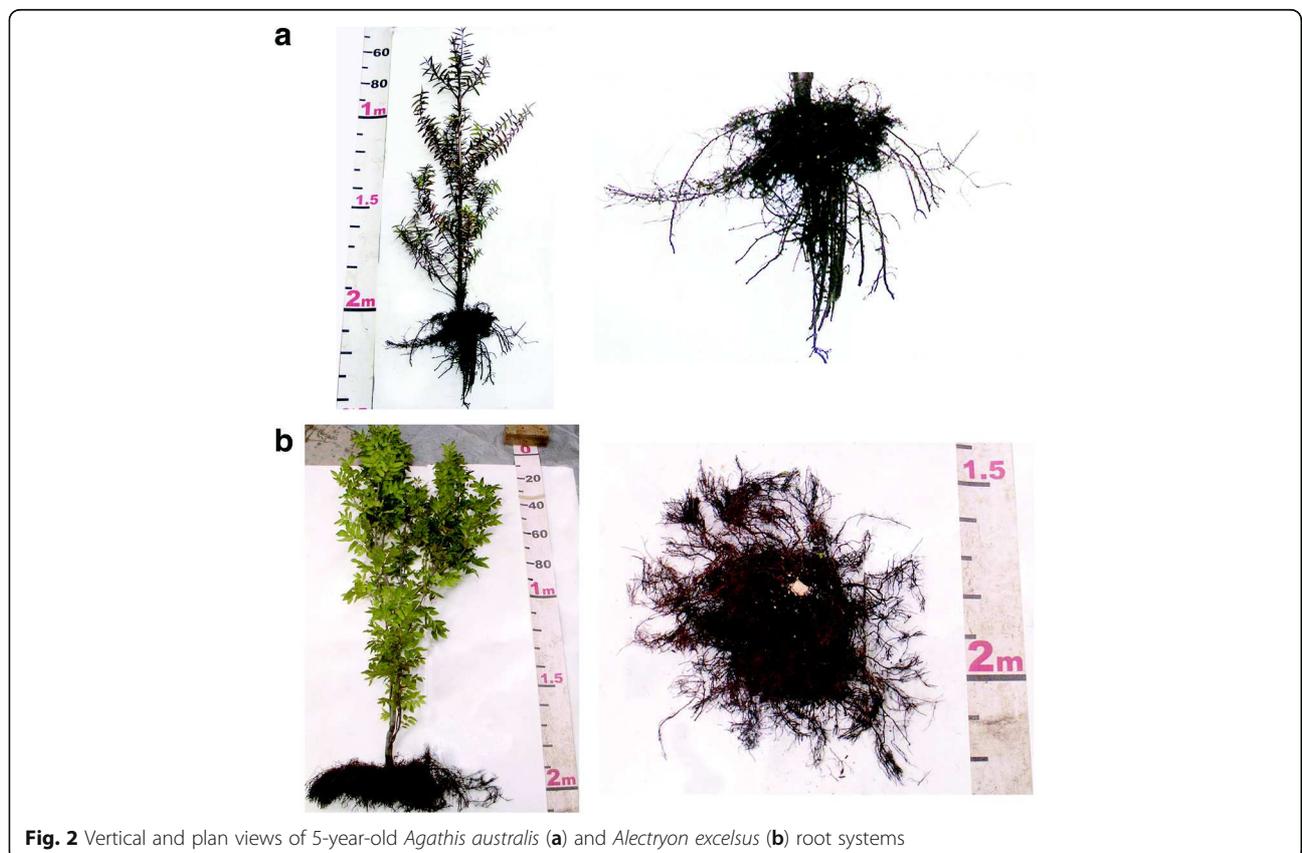
Table 1 Indigenous conifers and broadleaved species trialed and number of trees extracted each year of the trial

Botanical name Plant age (years)	Common name	Root system type	Number of plants extracted/species/year					Species total
			1	2	3	4	5	
Coniferous species								
<i>Agathis australis</i>	Kauri	Tap	10	10	10	10	10	50
<i>Dacrycarpus dacrydioides</i>	Kahikatea	Tap	10	10	10	10	10	50
<i>Dacrydium cupressinum</i>	Rimu	Tap	10	10	10	10	10	50
<i>Podocarpus totara</i>	Totara	Tap	10	10	10	10	10	50
<i>Prumnopitys ferruginea</i>	Miro	Plate	10	10	10	10	10	50
<i>Prumnopitys taxifolia</i>	Matai	Plate	10	10	10	10	10	50
Broadleaved species								
<i>Alectryon excelsus</i>	Titoki	Plate	10	10	10	10	9	49
<i>Vitex lucens</i>	Puriri	Tap	10	10	10	6	5	41
Annual total			80	80	80	76	74	390

weight loss was detectable then weighed to the nearest 0.1 g. The biomass and root:shoot ratio were calculated using dry mass. A carbon content of 50% of biomass is considered robust (Coomes et al. 2002). A conversion factor of biomass \times 1.65 (Williams 1978) was used to calculate carbon stocks (t CO₂). Carbon stock values do not include woody debris or fine litter.

Statistical analyses

ANOVA was used to determine the effects of year and species on above- and below-ground parameters. The Student-Newman-Keuls *post hoc* analysis was used to determine differences among the species within a year and among years when all species were averaged within each year. The normality of each analysis was determined by

**Fig. 2** Vertical and plan views of 5-year-old *Agathis australis* (a) and *Alectryon excelsus* (b) root systems

visual assessment of residual plots. The root biomass and root length data at 0.5-m radial intervals exhibited non-normality due largely to the prevalence of radial segments in which no or little root material was recorded for some of the root diameter size classes. The radially segmented root biomass and length data were therefore transformed using the equation $\log_e(x + c)$, where x was the root biomass or root length and c was 1.

Type-1 linear regression was used to fit RCD (overbark) and tree height data using the equation ($y = mx + c$). RCD was used instead of DBH in the analysis of tree allometry because many of the species were not expected to reach DBH height (1.4 m) for some years after the establishment of the trial. More importantly, it may serve as a better predictor of both above-ground and below-ground biomass quantities as root collar is measured at the intersection of above- and below-ground parameters and as stem taper in seedlings is minimal (Wagner and Ter-Mikaelian 1999). The relationship between RCD and foliage, branches and stem (Table 2), total above-ground biomass (AGB), total below-ground biomass (BGB), total root biomass (> 1- and > 2-mm diameter) and total root length (> 1- and > 2-mm diameter) (Table 3) was analysed using two-parameter exponential growth analysis using the equation $y = a \exp(bx)$, where b represented the slope of the regressions. The regression analyses include data for the containerised 1- and 2-year-old seedlings partitioned at the time the trial site was planted. All regression analyses were undertaken using SigmaPlot 12.5 (Systat Software, San Jose, CA).

Depending on the method of root extraction and focus of the research, regressions of total root biomass and length are often based on different groupings of root diameter size classes. For comparative New Zealand studies, some researchers have based their regressions on roots with a > 1-mm diameter (Phillips et al. 2015) while others have included only roots with a > 2-mm diameter (Watson and Tomblinson 2002, 2004; Marden et al. 2016). In this study, when regressed against RCD, a two-tailed, unpaired t test found no significant difference in the slopes of the

curves for roots with > 1- and > 2-mm diameter ($P = 0.741$). Therefore, regressions based on roots > 1-mm diameter were used for analyses of total root length and total root biomass. Unless otherwise stated, data are presented as a mean with standard errors, and statistical analyses were considered significant if $P \leq 0.05$.

Differences between the grouped conifers versus broadleaved species were not examined because they differ significantly in tree form; there were clear overlaps in above- and below-ground metrics between species across these groupings and because of the likely bias in analyses resulting from too few and/or uneven sample numbers.

Results

Allometric relationships

Tree height

Linear regression fitted the RCD and tree height data well, with r^2 ranging between 0.768 (*Vitex lucens*) and 0.916 (*Dacrydium cupressinum*), and all regressions were highly significant ($P < 0.001$; Fig. 3). There were significant differences among species with respect to height in each year (Additional file 2). With the exception of *Prumnopitys taxifolia*, which had the same average height in years 1 and 2 ($P = 0.05$; data not shown), the tree height of the remainder of species increased significantly from year to year. There was, however, no clear pattern as to which species had performed best until year 5 when *Prumnopitys taxifolia* (1.3 m), *Agathis australis* (1.6 m) and *Prumnopitys ferruginea* (1.6 m) were significantly shorter ($P = 0.05$) than the tallest two species *Podocarpus totara* (2.8 m) and *Dacrycarpus dacrydioides* (2.7 m), while *Vitex lucens* (2.4 m), *Dacrydium cupressinum* (2.2 m) and *Alectryon excelsus* (2.2 m) reached an intermediary height significantly different from the other species but not each other (Additional file 2).

Root collar diameter (RCD)

Differences in RCD among species in years 1–3 were variable, with no consistent species-specific trends other

Table 2 Allometric relationships between RCD against stem, branch and foliage biomass

Species	Stem			Branch			Foliage		
	r^2	P	Equation	r^2	P	Equation	r^2	P	Equation
<i>Agathis australis</i> (kauri)	0.822	< 0.001	$y = 6.958 \exp(0.114x)$	0.744	< 0.001	$y = 2.793 \exp(0.111x)$	0.799	< 0.001	$y = 5.661 \exp(0.106x)$
<i>Dacrycarpus dacrydioides</i> (kahikatea)	0.942	< 0.001	$y = 25.937 \exp(0.058x)$	0.908	< 0.001	$y = 16.919 \exp(0.064x)$	0.941	< 0.001	$y = 12.900 \exp(0.062x)$
<i>Dacrydium cupressinum</i> (rimu)	0.928	< 0.001	$y = 17.665 \exp(0.076x)$	0.798	< 0.001	$y = 13.086 \exp(0.074x)$	0.887	< 0.001	$y = 23.053 \exp(0.083x)$
<i>Podocarpus totara</i> (totara)	0.930	< 0.001	$y = 39.461 \exp(0.052x)$	0.699	< 0.001	$y = 35.461 \exp(0.058x)$	0.788	< 0.001	$y = 51.688 \exp(0.049x)$
<i>Prumnopitys ferruginea</i> (miro)	0.899	< 0.001	$y = 10.667 \exp(0.104x)$	0.868	< 0.001	$y = 8.871 \exp(0.115x)$	0.880	< 0.001	$y = 9.919 \exp(0.108x)$
<i>Prumnopitys taxifolia</i> (matai)	0.775	< 0.001	$y = 7.987 \exp(0.098x)$	0.790	< 0.001	$y = 26.804 \exp(0.106x)$	0.760	< 0.001	$y = 5.446 \exp(0.106x)$
<i>Alectryon excelsus</i> (titoki)	0.840	< 0.001	$y = 31.875 \exp(0.065x)$	0.840	< 0.001	$y = 14.277 \exp(0.0812x)$	0.734	< 0.001	$y = 26.199 \exp(0.052x)$
<i>Vitex lucens</i> (puriri)	0.786	< 0.001	$y = 48.929 \exp(0.035x)$	0.948	< 0.001	$y = 15.611 \exp(0.049x)$	0.950	< 0.001	$y = 25.903 \exp(0.042x)$

Table 3 Allometric relationships between RCD and total root length, and total root biomass for roots > 1 mm and > 2 mm diameter

Species	Root size class	Root length			Root biomass		
		r^2	P	Equation	r^2	P	Equation
<i>Agathis australis</i> (kauri)	> 1 mm	0.780	< 0.001	$y = 0.542 \exp(0.113x)$	0.879	< 0.001	$y = 1.173 \exp(0.137x)$
	> 2 mm	0.758	< 0.001	$y = 0.161 \exp(0.127x)$	0.860	< 0.001	$y = 0.879 \exp(0.144x)$
<i>Alectryon excelsus</i> (titoki)	> 1 mm	0.797	< 0.001	$y = 8.179 \exp(0.057x)$	0.851	< 0.001	$y = 17.629 \exp(0.062x)$
	> 2 mm	0.763	< 0.001	$y = 1.842 \exp(0.057x)$	0.851	< 0.001	$y = 11.206 \exp(0.066x)$
<i>Dacrycarpus dacrydioides</i> (kahikatea)	> 1 mm	0.783	< 0.001	$y = 12.159 \exp(0.045x)$	0.891	< 0.001	$y = 12.816 \exp(0.053x)$
	> 2 mm	0.704	< 0.001	$y = 3.090 \exp(0.047x)$	0.897	< 0.001	$y = 8.136 \exp(0.057x)$
<i>Dacrydium cupressinum</i> (rimu)	> 1 mm	0.816	< 0.001	$y = 2.743 \exp(0.080x)$	0.925	< 0.001	$y = 3.514 \exp(0.098x)$
	> 2 mm	0.829	< 0.001	$y = 0.527 \exp(0.088x)$	0.946	< 0.001	$y = 1.793 \exp(0.106x)$
<i>Podocarpus totara</i> (totara)	> 1 mm	0.461	< 0.001	$y = 11.481 \exp(0.040x)$	0.730	< 0.001	$y = 15.073 \exp(0.049x)$
	> 2 mm	0.659	< 0.001	$y = 1.921 \exp(0.046x)$	0.780	< 0.001	$y = 8.786 \exp(0.053x)$
<i>Prumnopitys ferruginea</i> (miro)	> 1 mm	0.831	< 0.001	$y = 2.731 \exp(0.095x)$	0.909	< 0.001	$y = 3.627 \exp(0.114x)$
	> 2 mm	0.855	< 0.001	$y = 0.357 \exp(0.112x)$	0.931	< 0.001	$y = 1.673 \exp(0.127x)$
<i>Prumnopitys taxifolia</i> (matai)	> 1 mm	0.779	< 0.001	$y = 2.699 \exp(0.101x)$	0.789	< 0.001	$y = 4.321 \exp(0.102x)$
	> 2 mm	0.515	< 0.001	$y = 0.359 \exp(0.124x)$	0.808	< 0.001	$y = 2.204 \exp(0.111x)$
<i>Vitex lucens</i> (puriri)	> 1 mm	0.812	< 0.001	$y = 13.037 \exp(0.037x)$	0.886	< 0.001	$y = 25.990 \exp(0.038x)$
	> 2 mm	0.723	< 0.001	$y = 4.002 \exp(0.033x)$	0.878	< 0.001	$y = 21.548 \exp(0.038x)$

than *Vitex lucens*, which, with the exception of year 4, had a larger RCD than the remaining species. In years 4 and 5, *Agathis australis*, *Prumnopitys taxifolia* and *Prumnopitys ferruginea* had a significantly smaller ($P = 0.05$) RCD (~20–24 mm) than *Dacrydium cupressinum* and *Alectryon excelsus* (~37–39 mm) (Additional file 2). Significantly larger still were *Podocarpus totara* and *Dacrycarpus dacrydioides*, with a similar RCD as each other (~48–50 mm), while *Vitex lucens* was the best performed of the trialled species with an RCD of 77.6 mm, almost twice that of the next best performed species and more than three times that of the slowest growing *Prumnopitys ferruginea* (Additional file 2).

Diameter at breast height (DBH)

There were significant differences among species with respect to DBH in year 5 (Additional file 2). The DBH of *Prumnopitys taxifolia* and *Prumnopitys ferruginea* were not significantly different from each other (2–3.9 mm) but *Prumnopitys taxifolia* had a significantly smaller ($P = 0.05$) DBH than did *Agathis australis* (8.0 mm), *Dacrydium cupressinum* (9.8 mm) and *Alectryon excelsus* (11.2 mm). *Dacrycarpus dacrydioides* (16.8 mm), *Podocarpus totara* (21.5 mm) and *Vitex lucens* (23.5 mm) each had a significantly larger ($P = 0.05$) DBH than did the other species but not compared with each other (Additional file 2).

Above-ground biomass (AGB)

Two-parameter exponential regression analysis was a good fit for the RCD and total AGB data, with r^2

ranging between 0.803 (*Agathis australis*) and 0.944 (*Dacrycarpus dacrydioides*), and all regressions were highly significant ($P < 0.001$) (Fig. 4). There was, however, no significant difference in mean total AGB among species until years 4 and 5, the exception being *Alectryon excelsus* which showed no further increase in mean total AGB ($P = 0.05$; data not shown). By year 5, the mean total AGB amassed by *Agathis australis* (251.1 g) and *Prumnopitys ferruginea* (381.4 g) were not significantly different from each other nor from *Prumnopitys taxifolia* (581.0 g). However, their biomass was significantly less ($P = 0.05$) than that of *Alectryon excelsus* (1092.3 g), *Dacrydium cupressinum* (1165.2 g) and *Dacrycarpus dacrydioides* (1231.0 g) and was exceeded only by *Podocarpus totara* (2142.9 g) and *Vitex lucens* (3026.0 g) (Fig. 5, Additional file 3).

Biomass allocation to foliage, branches and stem

Two-parameter exponential regression analysis was a good fit for RCD assessed against stem ($r^2 = 0.775–0.944$), branches ($r^2 = 0.699–0.948$) and foliage ($r^2 = 0.734–0.950$) biomass, and all regressions were highly significant ($P < 0.001$) (Table 2). There were significant differences ($P = 0.05$) among species in the allocation of biomass between foliage, branches and stem in each year of the trial (Additional file 3). At 5 years of age, *Agathis australis*, *Dacrycarpus dacrydioides*, *Prumnopitys ferruginea*, *Alectryon excelsus* and *Vitex lucens* had the highest proportion of their total AGB allocated to the stem (35–49%), branches (19–40%) and least to foliage (20–32%). Exceptions to this general trend were *Dacrydium*

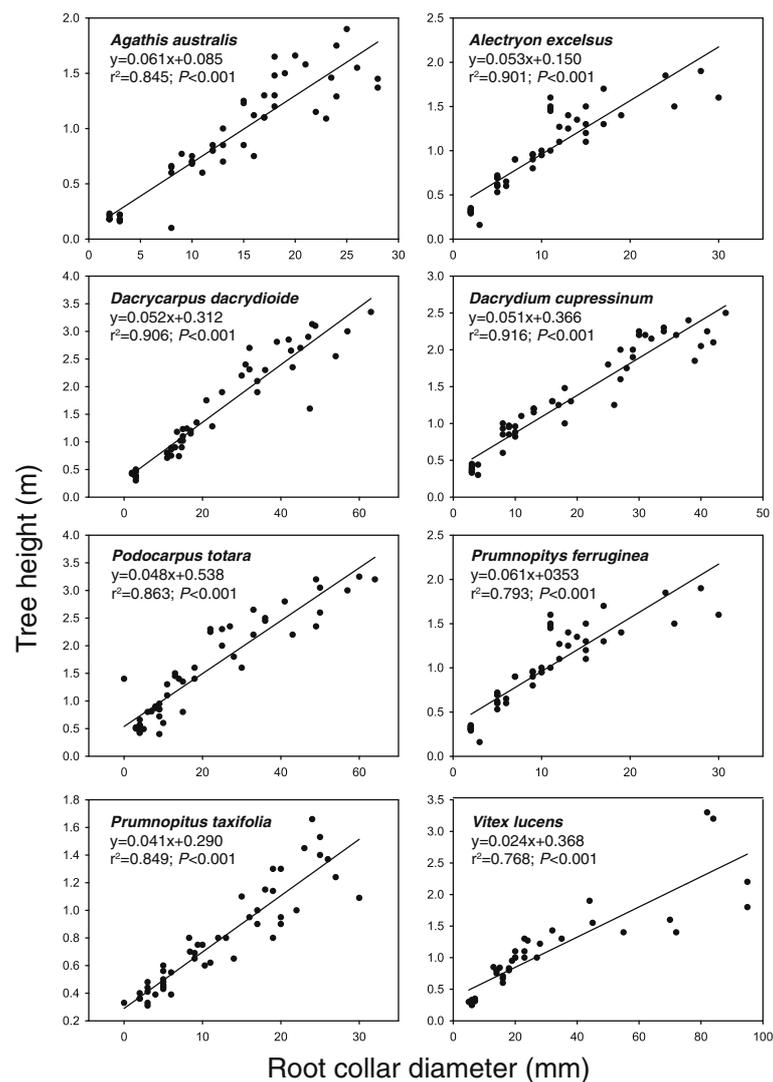


Fig. 3 Linear regression analysis of RCD and tree height. Note that the scale on the y and x axes differs between species

cupressinum with a disproportionate 51% of its total AGB allocated to foliage comprising scale leaves closely appressed to the stem (Wardle 2002). Also, for *Prumnopitys taxifolia* and *Podocarpus totara* with deep, narrow crowns and short lateral branches, 69 and 37% of their respective total AGB was allocated to branches (Additional file 3).

Below-ground biomass (BGB)

Similarly, two-parameter exponential regression analysis was a good fit for the RCD and mean total BGB data, with r^2 ranging between 0.757 (*Podocarpus totara*) and 0.946 (*Dacrydium cupressinum*), and all regressions were highly significant ($P < 0.001$) (Fig. 6). Additionally, there were significant differences ($P = 0.05$) between species in the allocation of biomass between root mass and root bole in each year of the trial (Additional file 5).

The differences in mean total BGB among species in 1- and 2-year-old seedlings were initially small, but it became more significant in years 4 and 5 ($P = 0.05$; data not shown), when the majority of species showed a significant increase in mean total BGB. Exceptions to this general pattern include *Agathis australis*, with no increase in mean total BGB in years 1 and 2, a modest increase in year 3 and no increase in year 4, and in year 5, the increase in mean total BGB was significantly greater than in any of the previous years. By year 5, *Agathis australis* (72.0 g) had a significantly less ($P = 0.05$) mean total BGB than both *Prumnopitys ferruginea* (134.9 g) and *Prumnopitys taxifolia* (134.6 g). For the remaining species, the mean total BGB of *Dacrycarpus dacrydioides* (371.2 g), *Dacrydium cupressinum* (397.4 g), *Alectryon excelsus* (402.2 g) and *Podocarpus totara* (450.0 g) was significantly different again but not to each

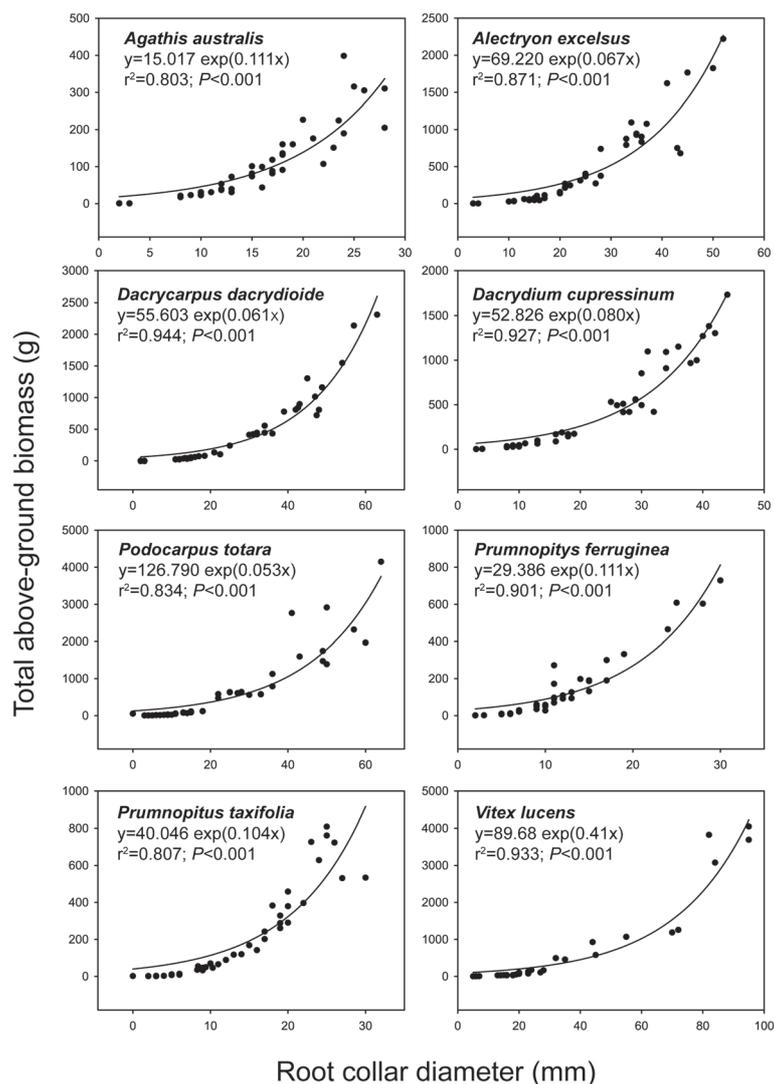


Fig. 4 Exponential growth analysis of RCD and total above-ground biomass. Note that the scale on the y and x axes differs between species

other. *Vitex lucens* (1257.4 g) had the highest mean total BGB and was significantly different ($P = 0.05$) from all the other species (Fig. 5, Additional file 3).

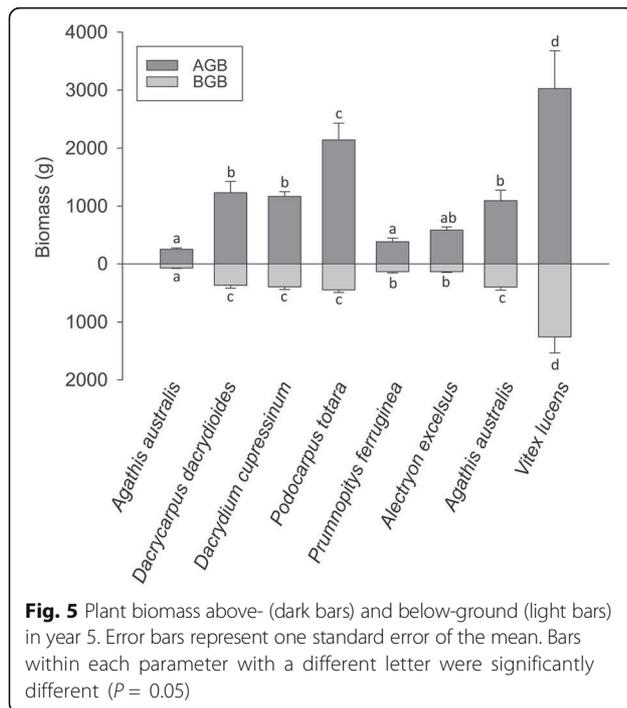
Biomass allocation to root and root bole

For the majority of species, there were no significant interspecies differences in the allocation of mean root and root bole biomass until years 4 and 5, at which time both root and root bole biomass increased significantly ($P = 0.05$; data not shown), similar to the pattern for the allocation of mean total BGB and AGB. For *Agathis australis*, the increase in root and root bole mass occurred in year 3, whereas for *Prumnopitys ferruginea* and *Vitex lucens*, it did not increase until year 5. By year 5, *Vitex lucens* had the largest root bole biomass (287.3 g) but was not significantly different to *Dacrycarpus dacrydioides* (112.7 g), *Alectryon excelsus* (105.8 g),

Podocarpus totara (103.0 g) and *Dacrydium cupressinum* (102.6 g). In contrast, the mean total root bole biomass of the conifers *Agathis australis* (17.2 g), *Prumnopitys ferruginea* (22.2 g) and *Prumnopitys taxifolia* (22.9 g), though not significantly different from each other, are each an order of magnitude less than for the remainder of the conifers and broadleaved species (Additional file 5). *Vitex lucens* also had the greatest root biomass (970.1 g, 79.3% of total BGB), while *Agathis australis* had the least (54.8 g, 75.2% of total BGB). For all species, the proportion of the total BGB allocated to the roots (69–84%) was greater than that allocated to the root bole (16–31%).

Root biomass distribution by depth and radius

For all species in each year of the trial, 100% of the total BGB ($P < 0.001$) was confined to the 0–0.5-m depth



increment, and inter-species differences ($P = 0.05$) in the mean maximum rooting depth were minimal. For most species, this had increased from ~ 0.1 m in year 1 to ~ 0.3 m by year 5 (Additional file 4). For any individual seedling, the tap-rooted *Agathis australis* developed the deepest (0.7 m) root, while the plate-rooted systems of *Prumnopitys taxifolia*, *Prumnopitys ferruginea* and *Alectryon excelsus* had the shallowest root systems (~ 0.15 m). By year 5, the mean maximum root depth of each of the trialled species was similar, whether conifers or broad-leaved species and tap-rooted or plate-rooted species (Additional file 4).

Similarly, for the first 3 years, 100% of the total BGB ($P < 0.001$) of all species was confined to within a 0.5-m radius of the root bole. By year 4, only *Dacrycarpus dacrydioides*, *Alectryon excelsus* and *Vitex lucens* had extended their roots to a radius of between 1.0 and 1.5 m from the root bole (Additional file 7). The root mass and percentage of total root mass of *Dacrycarpus dacrydioides* (0.8 g, 0.4%) and *Alectryon excelsus* (0.9 g, 0.2%) at this distance were not significantly different from each other but were significantly different from *Vitex lucens* (3.4 g, 1.7%). *Vitex lucens* was the only species by year 5 to have extended its root network to a radius of between 1.5 and 2.0 m from the root bole; however, the roots comprised only 8.3 g, 0.8% of its total root mass. Between years 1 and 5, *Agathis australis* was the only species to have 100% of its root mass confined to within 0.5 m of the root bole. At year 5, $> 90\%$ of the total root mass of *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Prumnopitys taxifolia*, *Prumnopitys ferruginea*

and *Alectryon excelsus* occurred within a 0.5-m radius of the root bole, *Podocarpus totara* 76.8% and *Vitex lucens* 65.9% (Fig. 7, Additional file 6).

Root biomass allocation by root diameter size class

Exponential regression analysis of RCD and total root biomass for roots > 1 - and > 2 -mm diameter size class showed very similar regressions (Fig. 8), with RCD explaining between 73 and 92% of the variation in root biomass for roots > 1 mm and between 78 and 94% for roots > 2 mm (Table 3).

In year 5, fibrous roots accounted for the highest proportion of the total root mass of each of the plate-rooted species *Alectryon excelsus* (23.5%), *Prumnopitys ferruginea* (56.4%) and *Prumnopitys taxifolia* (49.7%) (Fig. 9). Similarly, for the tap-rooted species, fibrous roots accounted for between 28.1% (*Dacrycarpus dacrydioides*) and 49.3% (*Dacrydium cupressinum*) of their total root mass. For all species, the percentage of fibrous root biomass decreased as root sizes increased with increasing plant age. The largest root diameter size class (50–100 mm) was recorded for *Vitex lucens* only and comprised $< 2\%$ of its total root biomass. For the remainder of the species, the largest root diameter size class was 20–50 mm and comprised just 0.1% of *Prumnopitys ferruginea* and 6.8% of the total root mass (largely tap root) of *Agathis australis*.

BGB/AGB ratio

In year 1, although the BGB/AGB ratio was highest for the tap-rooted *Vitex lucens* (0.89) and lowest for the plate-rooted *Prumnopitys taxifolia* (0.25), there was no consistent relationship between this ratio and root type from year to year (Additional file 3). By year 5, *Podocarpus totara* (0.21) and *Prumnopitys taxifolia* (0.23) had the lowest BGB/AGB ratio, and although for *Vitex lucens* the BGB/AGB ratio remained the highest of the trialled species (Fig. 5), it had halved to 0.42 by year 5. Similarly, a decline in BGB allocation with increasing age was apparent in *Podocarpus totara* (0.47 in year 1, decreasing to 0.21 in year 5) and *Prumnopitys ferruginea* (0.5 in year 1, decreasing to 0.35 in year 5). Averaged across all eight species, the BGB and AGB was 0.32 and 0.68, respectively.

Root length and root system dimensions (diameter)

Exponential growth analyses of RCD and total root length fitted least well for *Podocarpus totara* with RCD explaining 46 and 66% of the variation in root length for roots > 1 and > 2 mm, respectively. In contrast, this relationship fitted best for *Prumnopitys ferruginea* with RCD explaining between 83 and 85% of the variation in root length for roots > 1 mm and > 2 mm, respectively. (Table 3, Fig. 10).

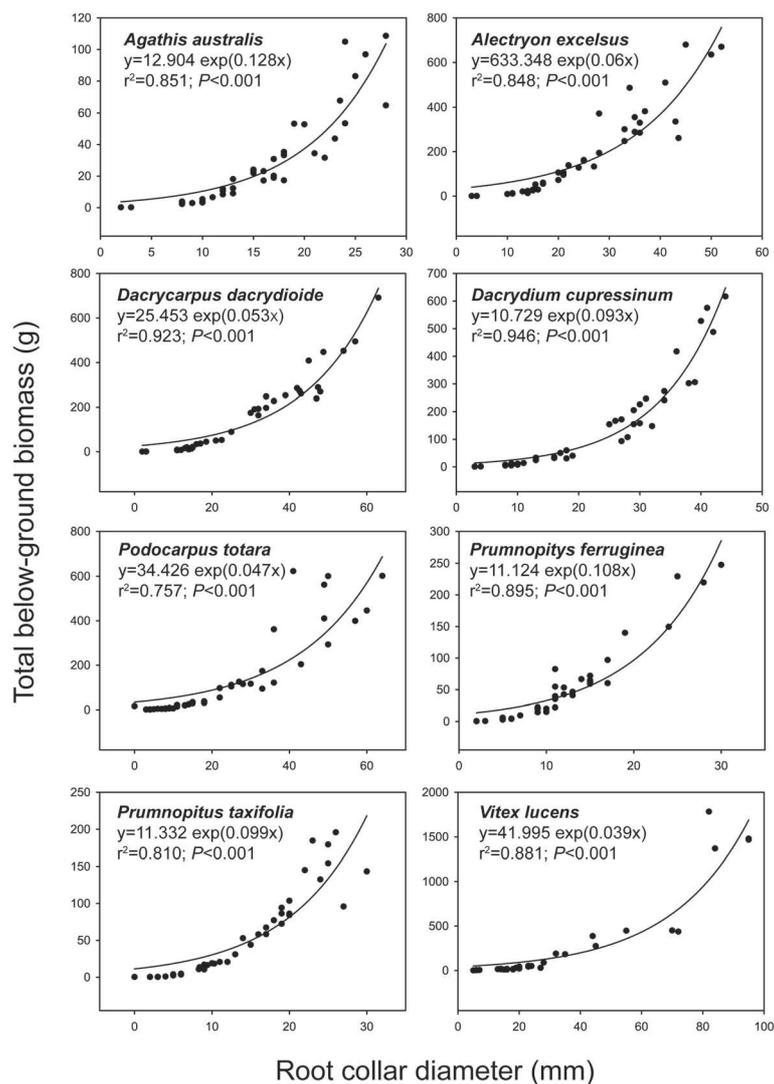


Fig. 6 Exponential growth analysis of RCD and total below-ground biomass. Note that the scale of the y and x axes differs between species

At year 1, none of the species had produced roots > 1-mm diameter. By year 2, *Alectryon excelsus* and *Vitex lucens* each produced > 2.5 m of root, significantly more ($P = 0.05$) than *Dacrycarpus dacrydioides* (~ 2 m), which in turn was significantly more than that of each of the remaining species at < 1 m of root length (Additional file 4). By year 5, the total root length for each species increased substantially and differences between species became more pronounced. For example, *Agathis australis* produced the least mean total root length (9.01 m) while *Vitex lucens* (347.45 m) at the same age produced two orders of magnitude more root length (Additional file 4).

In years 2 and 3 of the trial, and for each of the species trialled, 100% of the total root length occurred within a 0.5-m radius of the root bole, and for *Agathis australis*, this was the case through to year 5 (Fig. 11, Additional file 7). By year 4, only *Dacrycarpus dacrydioides*, *Alectryon*

excelsus and *Vitex lucens* had extended their roots into the 0.5–1.0-m radial sector where *Vitex lucens* had a significantly greater proportion ($P = 0.05$) of its total root length (34%) at this radial distance than did *Dacrycarpus dacrydioides* (19%) and *Alectryon excelsus* (17%). Similarly, at 1.0–1.5-m radial distance from the root bole, *Vitex lucens* had significantly more ($P = 0.05$) of its total root length (~ 5%) than did *Dacrycarpus dacrydioides* (1%) and *Alectryon excelsus* (0.4%).

For all species, in years 1 and 2, there was little inter-species difference in mean root system dimensions (i.e. mean maximum root spread). However, by year 5, of the broadleaf species, *Vitex lucens* had developed a significantly greater ($P = 0.05$) mean maximum root spread (2.5 m) than had *Alectryon excelsus* (1.6 m), and its root spread was also significantly greater than that of the largest of the conifer root systems, i.e. that of *Podocarpus*

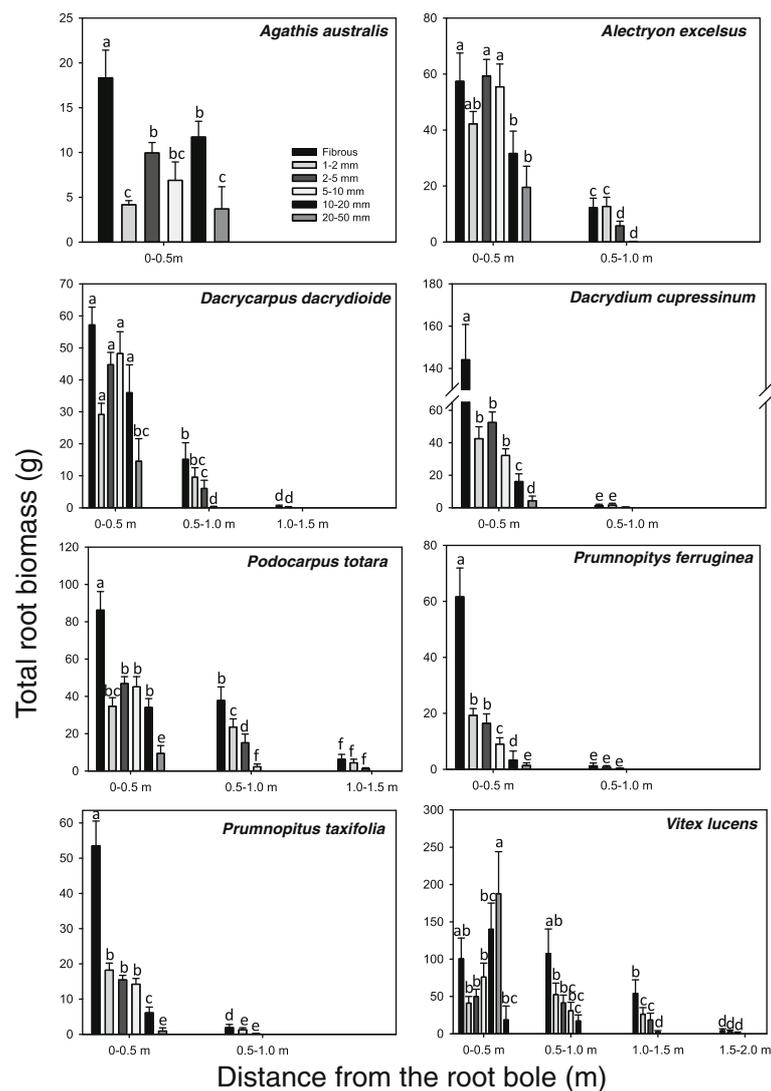


Fig. 7 Distribution of total root biomass with increasing radial increments from the root bole. Note that the scale on the y axis differs between species

totara (2.2 m) (Additional file 4). The mean maximum root spread of both *Alectryon excelsus* and *Dacrycarpus dacrydioides* (1.7 m), while not different from each other, was significantly larger ($P = 0.05$) than the more compact root systems of *Prumnopitys taxifolia* (1.2 m), *Prumnopitys ferruginea* (1.0 m) and *Dacrydium cupressinum* (1.1 m), which in turn were not significantly different from each other. The mean maximum root spread of *Agathis australis* (0.5 m) was significantly smaller than that of the remainder of species trialled (Additional file 4).

Root length by root diameter size class

For all the trialled species, the highest proportion of the total root length of 5-year-old trees was in the 1–2-mm-diameter size class and with the exception of *Agathis australis* comprised >70% of their total root length. For *Agathis australis*, 39% of its total root length

comprised roots in the 2–5-mm size class, 20% greater than for the remainder of species (Fig. 12). The percentage of total root length decreased with increasing root size class, and for the 20–50-mm size class, where present, roots comprised $\leq 1.5\%$ of the total root length. None of the trialled species had roots in the >50-mm diameter size class.

Plant biomass and carbon accumulation

For each of the species trialled, the mean annual total biomass of individual trees increased significantly (Additional file 3). By year 5, the slowest growing of the trialled species including *Agathis australis*, *Prumnopitys ferruginea* and *Prumnopitys taxifolia* each accumulating the least total biomass of $\sim 0.32 \text{ kg tree}^{-1}$ (0.16 kg of C), $\sim 0.56 \text{ kg tree}^{-1}$ (0.26 kg of C) and $\sim 0.72 \text{ kg tree}^{-1}$ (0.36 kg of C), respectively. Conversely, *Dacrycarpus*

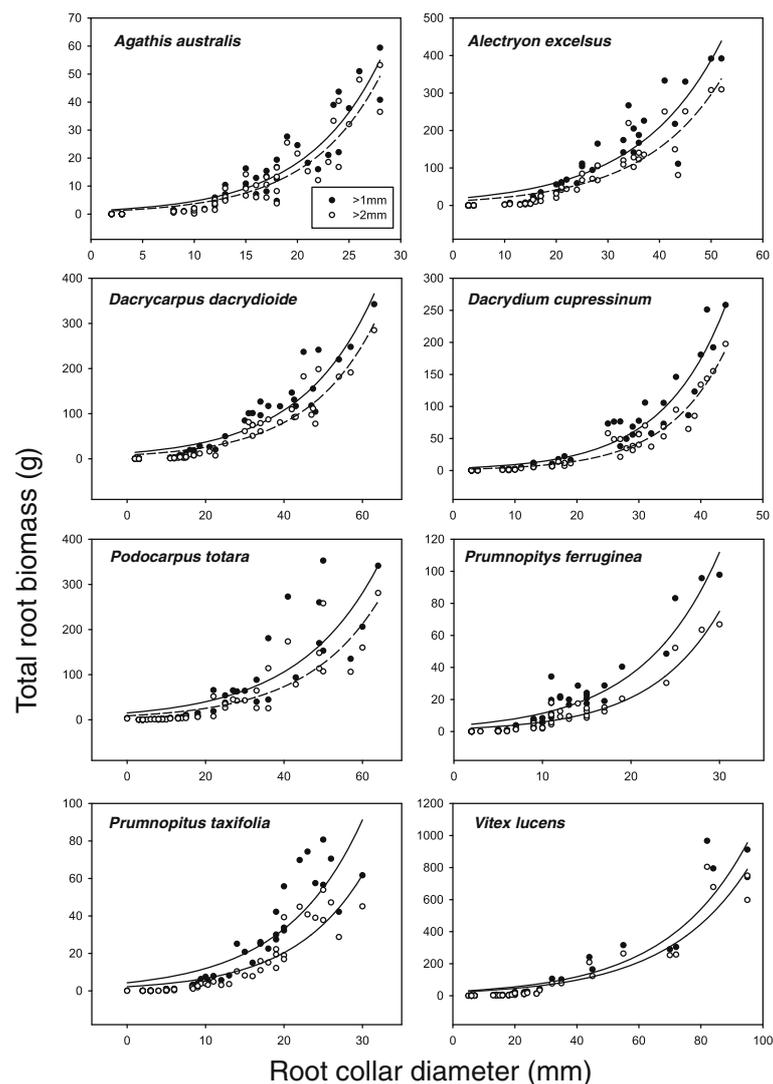


Fig. 8 Exponential growth analysis of RCD and total root biomass. Note that the scale of the y and x axes differs between species

dacrydioides, *Dacrydium cupressinum* and *Alectryon excelsus* each accumulated $\sim 1.56 \text{ kg tree}^{-1}$ (0.78 kg of C), while the highest biomass accumulation was by *Podocarpus totara* $\sim 2.59 \text{ kg tree}^{-1}$ (1.30 kg of C) and *Vitex lucens* $\sim 4.28 \text{ kg tree}^{-1}$ (2.14 kg of C) (Table 4).

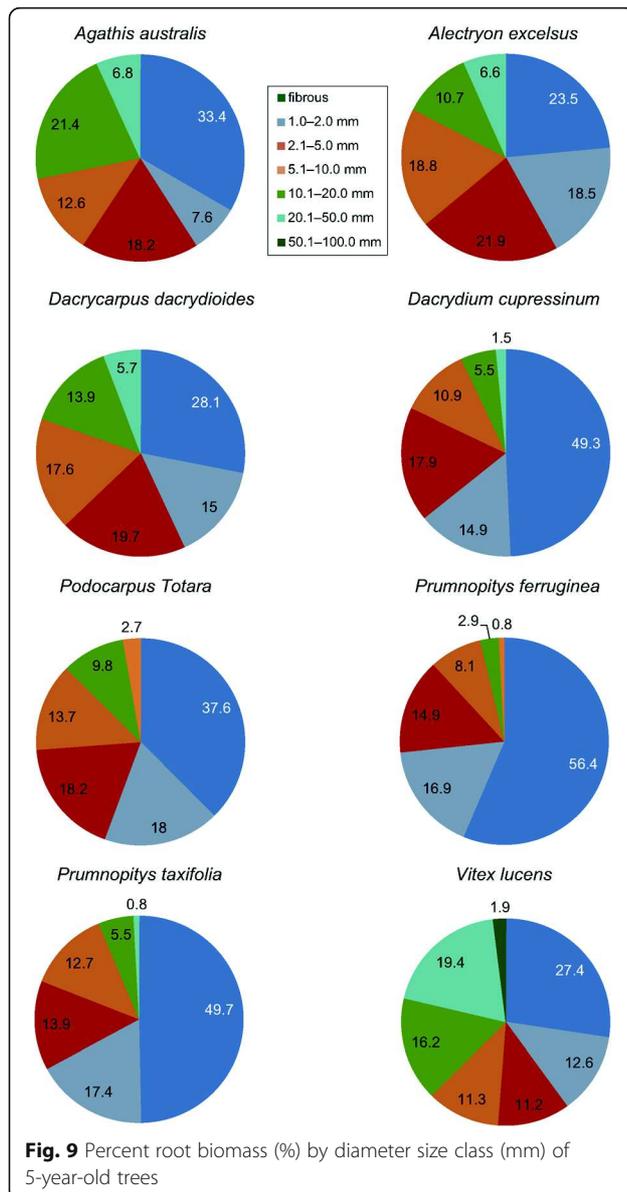
Root system types

Two types of root systems (tap-rooted and plate-rooted) were observed based on the descriptive classification of Hinds and Reid (1957) we recognised.

Of the trialled species that developed a tap root (*Agathis australis*, *Dacrycarpus dacrydioides*, *Vitex lucens*, *Podocarpus totara* and *Dacrydium cupressinum*), the seedling radicle of *Agathis australis* (Fig. 2a) was prominent earliest (3-year-old plants) and extended deeper (0.3 m) than the remainder of the trialled species. By year 5, *Podocarpus totara*

produced the longest laterals extending a distance of 2.2 m, significantly longer ($P=0.05$) than all the other trialled species, and of the broadleaved species, *Vitex lucens* attained the greatest mean root spread (2.5 m) (Additional file 4).

Plate-rooted species include the conifers *Prumnopitys taxifolia* and *Prumnopitys ferruginea* and the broadleaved *Alectryon excelsus*. Their juvenile root systems are compact and consist largely of abundant fibrous and numerous short, gnarly, lateral roots of small diameter size ($< 1 \text{ mm}$ diameter) somewhat resembling that of *Agathis australis* but lacking a tap root (Fig. 2b). Of the plate-rooted species, the broadleaved *Alectryon excelsus* developed the longest lateral roots by year 5 with a spread of 1.6 m, significantly longer ($P=0.05$) than the other plate-rooted species (Additional file 4).



Discussion

Plant allometry

The physiological age of all the species was similar at the time of planting, but there were initial and significant differences in the above-ground metrics among species. Once established, interspecies differences in year-on-year growth remained but became increasingly variable. Payton et al. (2009)⁵ suggested that AGB should be estimated using height and percentage cover for juvenile trees with a DBH < 50 mm. More recently, Mason et al. (2014) used tree height and basal area to determine AGB in New Zealand shrublands while Beets et al. (2012) used a two-factor exponential model which uses DBH or $DBH^2 \times \text{height}$ to estimate AGB biomass in mature native forests. Magalhães (2015) suggested that

DBH is preferential to RCD as RCD can be affected by root buttress. However, RCD was used in the current study as DBH height (1.4 m) of the juvenile species trialled was not attained until year 4. Indeed, as suggested by Wagner and Ter-Mikaelian (1999), RCD may serve as a better predictor of both the above- and below-ground biomass as it is measured at the intersection of the base of the stem with the root bole. In fact, RCD provided the best fit for tree height and total AGB, and all regressions were highly significant in each of the 5 years of the current trial and for all the trialled species.

To date, generic rather than species-specific allometric equations have been used to estimate the AGB of mature indigenous forest and shrub biomass. Extrapolating these equations to juvenile plants with smaller diameters far outside the range of data used to develop them is questionable however (Claesson et al. 2001; Zianis and Mencuccini 2003). The allometric biomass equations presented in this paper indicate that there are clear differences in growth performance among species, at least at their juvenile stage, and that different fitted coefficients are required. Furthermore, there is a dearth of allometric equations for estimating the below-ground biomass of indigenous species. The absence of empirical data means that a figure of 20% is widely accepted, both locally (Beets et al. 2007) and internationally (Coomes et al. 2002) despite the precision of these root estimates tending to be low (Hall et al. 2001).

Studies that include measurements of both the above- and below-ground growth attributes of the juvenile form of different species have also found RCD to be a good fit for estimating height, AGB and also BGB. For example, Marden et al. (2018; in press) found RCD to be a good fit for estimating all three attributes of 12 of New Zealand's indigenous riparian species with each species requiring a specific fitted coefficient. Furthermore, Marden et al. (2016) found that two-parameter exponential regressions using RCD was successful in predicting the BGB of five seed lots of *Pinus radiata* between 1 and 4 years old with RCD explaining between 93 and 98% of the variability in BGB. Similarly, Phillips et al. (2015) found it possible to develop simple relationships between RCD and growth attributes with reasonable r^2 values for below-ground biomass and total root length.

However, year-on-year growth performance data for the juvenile stage of most of New Zealand's indigenous species is particularly rare, thus limiting comparisons with other published works. Nonetheless, there is evidence to show that the proportion allocated to BGB decreases with increasing age despite significant year-on-year gains in total plant biomass in many species, both indigenous and exotic (Marden et al. 2005). This concurs with other local (Watson et al. 1995, 1999) and international (Abernethy and Rutherford 2001;

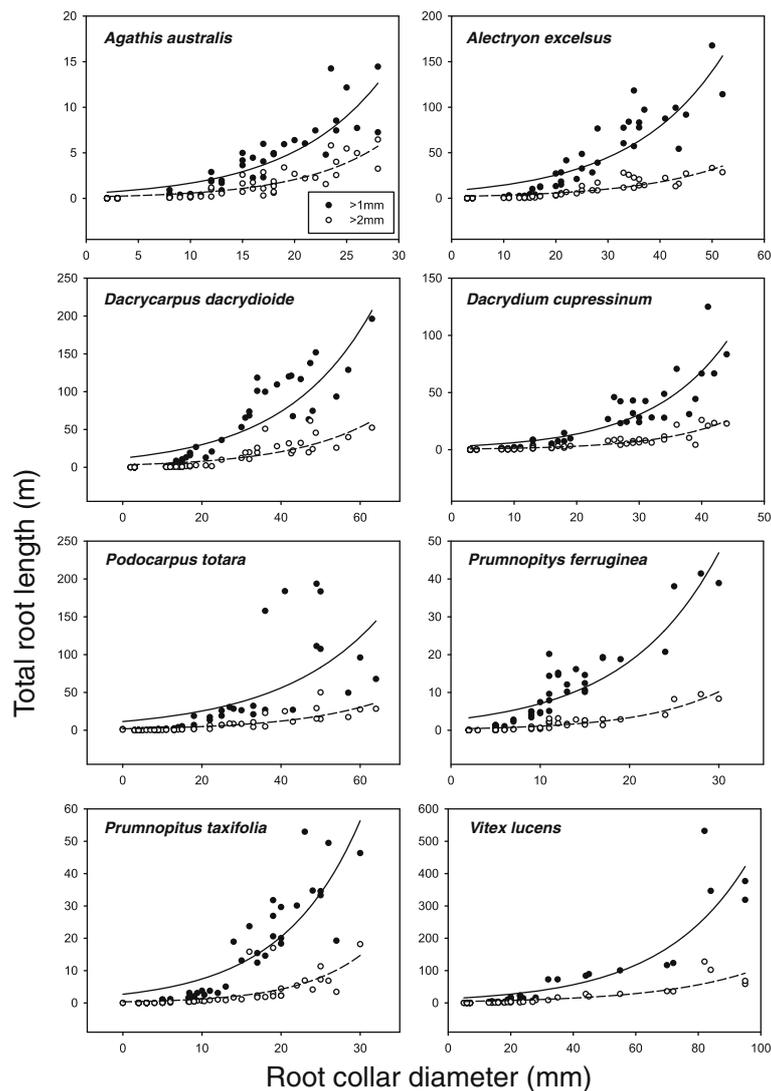


Fig. 10 Exponential growth analysis of RCD and total root length. Note that the scale of the y and x axes differs between species

Easson and Yarbrough 2002) studies where a decrease in the root/shoot ratio for small saplings has been related to an increase in plant size (Kira and Shidei 1967; Walters and Reich 1996) and to an increase in plant height (Cao and Ohkubo 1998). Conversely, Marden et al. (2016) found no clear indication that the root/shoot ratio of 1- to 4-year-old *Pinus radiata* decreased over this period but instead remained relatively constant. Biomass allocation to components of woody plants is also affected by factors including plant architecture and morphology and climatic and edaphic factors (Ketterings et al. 2001).

In this study, the range of biomass apportioned to below-ground components by year 5 was 23–41%, not dissimilar to that of 12 early colonising indigenous species at the same age with a below-ground biomass of between 24 and 44% (Marden et al.

2005) or for 3-year-old *Eucalyptus fastigata* (33%), *Sequoia sempervirens* (29%), *Acacia melanoxylon* (37%) and *Pinus radiata* (36%) trialled at the same site (Phillips et al. 2015). Although the below-ground biomass of each of five different 5-year-old clones of *Pinus radiata* (~22%) established on steep hill country (Marden et al. 2016) is at the lower end of this range, it is nonetheless consistent with that established for similar-aged pines planted at a range of sites in New Zealand (Watson and Tomblinson 2002, 2004) and likely reflects harsher site and edaphic and climatic factors.

There was no consistent year-to-year difference in the root/shoot ratio between the tap- and plate-rooted species or between conifers and broadleaved species (Additional file 3).

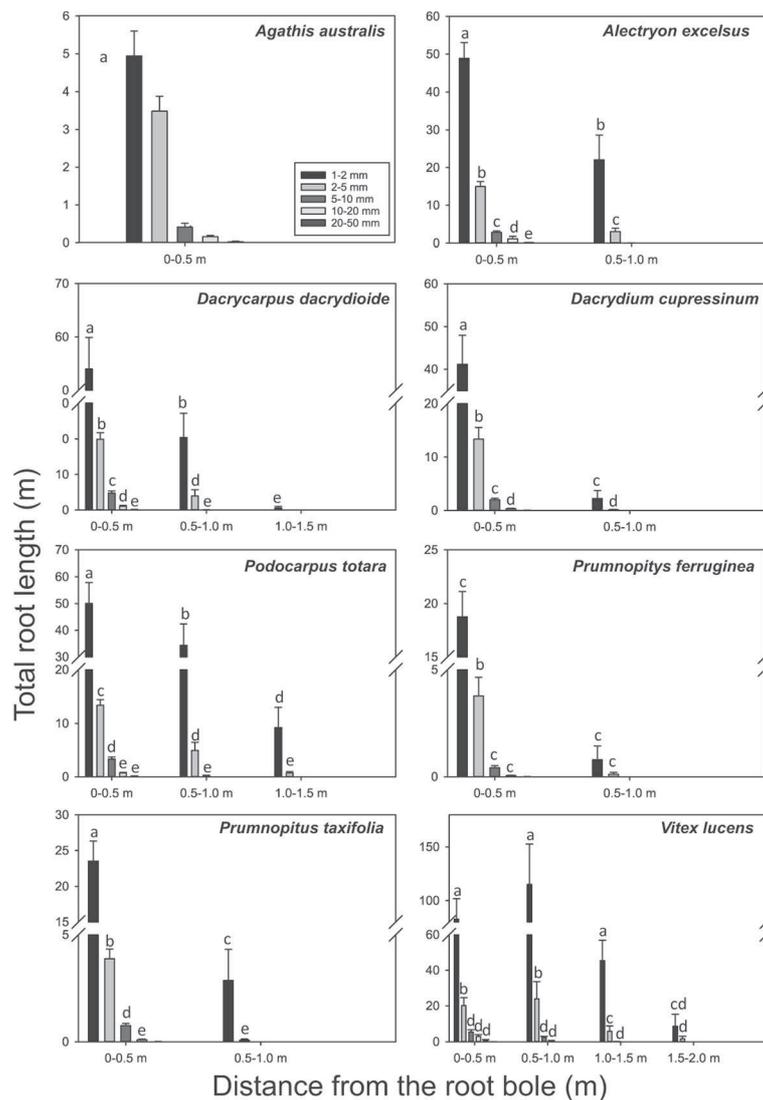


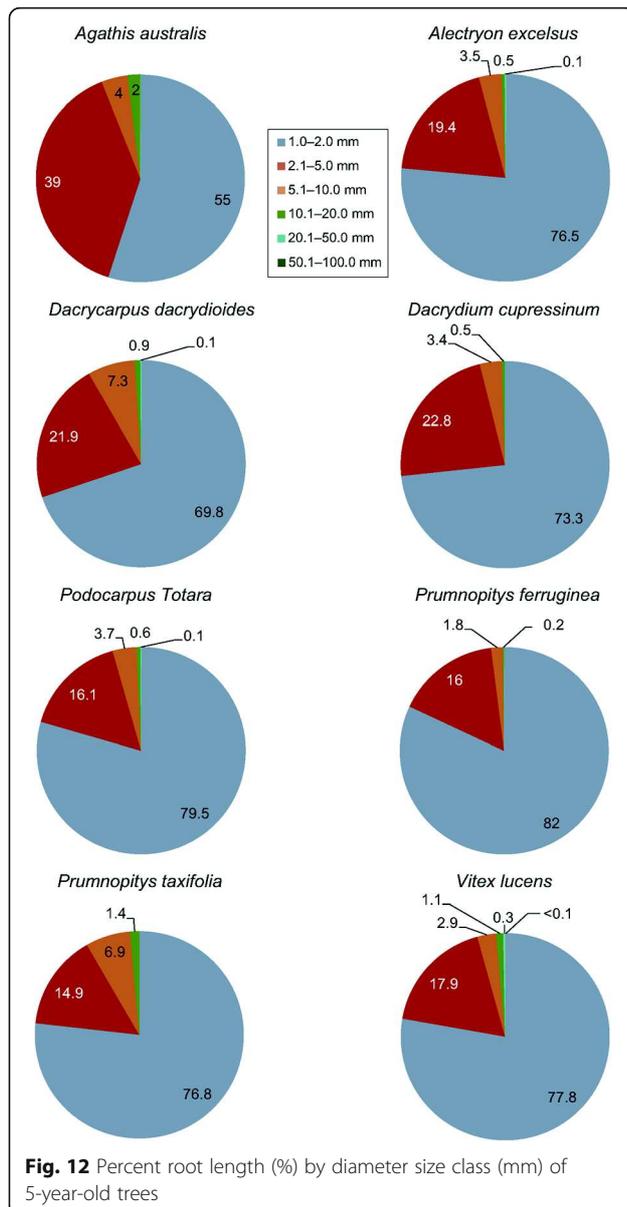
Fig. 11 Distribution of total root length with increasing radial increments from the root bole. Note that for the species with the greatest total root length there is a break in the y axis scale

Root metrics and architecture

Published accounts on the architecture of root systems of New Zealand's commonest and longest-lived native conifer and broadleaved forest species are scarce, descriptive and generally based on observations of partially exposed roots undermined along river banks (Cameron 1963) or of root boles of windthrown trees (Bergin and Steward 2004). At the time of establishing this trial, there were no root-related data (photographic or descriptive) for juvenile specimens of the trialed species. While some of the general findings on root distribution (depth and spread) reported here were anticipated from the results of a previous trial at the same site (Marden et al. 2005), other findings were not. For example, it was anticipated that a high proportion of the total BGB ($P <$

0.001) would likely remain confined to the 0–0.5-m depth increment, to within a 0.5-m radius of the root bole even in the absence of barriers to root penetration. Also expected was that root biomass and root length would decrease with increasing depth and horizontal distance from the root bole. Similarly, fibrous roots (as a percentage of total root biomass) were expected to decrease as root sizes increased.

Conversely, while excavations of the root systems of juvenile *Agathis australis* revealed the known presence of a well-developed tap root (Bergin and Steward (2004), the presence of a tap root in *Dacrycarpus dacrydioides*, *Vitex lucens*, *Podocarpus totara* and *Dacrydium cupressinum* was unexpected and has not to our knowledge been previously reported. Additionally, their many



leading lateral roots, though initially of small diameter, were highly symmetric; thus, few areas of soil were left totally devoid of any roots. These species typically had a high number of roots per unit volume of soil and, as expected for juvenile plants, the bulk of their root mass and total root length was confined to a shallow depth and within close proximity to the root bole. By comparison, the root systems of the juvenile plate-rooted species (including the conifers *Prumnopitys taxifolia* and *Prumnopitys ferruginea* and the broadleaved *Alectryon excelsus*) typically had fewer lateral roots but were of larger diameter and with limited branching tended to developed in preferential directions. Thus, the number of roots per unit volume of soil was lower than for the tap-rooted species with significant areas of soil

remaining devoid of root mass. This was also observed during the excavation of root systems of non-native forest species (Phillips et al. 2015) and non-native *Populus* and *Salix* species at the same trial site (Phillips et al. 2014). These results suggest that interspecies differences in the distribution of roots and their overall root system architecture are likely to be inherent rather than due to seedling propagation, planting practices or site factors given that there were no observable differences in the physical attributes of the soil across this essentially flat terrace surface and competing influences from adjacent well-spaced plants were unlikely.

Conversely, the highly asymmetric root architecture of juvenile *Pinus radiata* reported by Marden et al. (2016) is considered typical of tree root systems developed on steep slopes where the greatest proportion of the total root length trends in diagonally opposite directions previously referred to as bilateral fan-shaped architecture (Chiatante et al. 2003). Here, the larger and stronger lateral roots develop in the upslope (Schiechtel 1980) under compression (Stokes and Guitard 1997) and provide the greatest contribution to tree stability/anchorage (Sun et al. 2008). Roots located in the downslope direction develop under tension, and are therefore smaller and weaker, and likely contribute less to tree anchorage. Nicoll and Ray (1996) reported that prevailing winds can influence the distribution of the structural roots of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) where, relative to the prevailing wind, there were more roots located on the leeward side than on the windward side of trees. Marden et al. (2016) considered the development of the bilateral fan-shaped distribution of structural roots of *Pinus radiata* to have been influenced by the predominance of northerly winds as an adaptation to improve the rigidity of the soil-root plate and to counteract their vulnerability to windthrow.

The openness and exposure of the conifer and broad-leaved species trial site to strong winds resulted in stem breakage of *Alectryon excelsus*, and *Vitex lucens* was defoliated during periods of heavy frost. However, site factors are unlikely to have contributed to inter-species differences in their overall growth performance as all the trialled species tolerate a wide range of environmental conditions. Furthermore, with weed control, unlimited water availability, a fertile alluvial soil and the absence of barriers to root development, the resultant growth performance could be considered as optimal for these species. However, as is common with nursery-raised juvenile plants, factors such as wrenching, root trimming and planter bag constriction likely stunt the rate of root biomass accumulation, root spread and depth within the first 3 years following planting (Marden et al. 2005). To what extent minor root binding affected the eventual distribution of root diameter size classes

Table 4 Mean tree biomass (dry weight), carbon content (kg) and carbon stock (t CO₂/1000 stems per hectare) for 5-year-old trees

Botanical name	Common name	Mean tree biomass (kg)	Carbon content (kg)	Carbon stock (t CO ₂ /1000 spha)
Coniferous species				
<i>Agathis australis</i>	Kauri	0.32 (0.03) ^a	0.16 (0.02) ^a	0.53 (0.05) ^a
<i>Dacrycarpus dacrydioides</i>	Kahikatea	1.60 (0.24) ^{bc}	0.80 (0.12) ^{bc}	2.64 (0.40) ^{bc}
<i>Dacrydium cupressinum</i>	Rimu	1.56 (0.13) ^c	0.78 (0.06) ^c	2.58 (0.21) ^c
<i>Podocarpus totara</i>	Totara	2.59 (0.32) ^d	1.30 (0.16) ^d	4.28 (0.53) ^d
<i>Prumnopitys ferruginea</i>	Miro	0.52 (0.09) ^a	0.26 (0.04) ^a	0.85 (0.15) ^a
<i>Prumnopitys taxifolia</i>	Matai	0.72 (0.07) ^{ab}	0.36 (0.03) ^{ab}	1.18 (0.12) ^{ab}
Broadleaved species				
<i>Alectryon excelsus</i>	Titoki	1.49 (0.23) ^c	0.75 (0.12) ^c	2.47 (0.39) ^c
<i>Vitex lucens</i>	Puriri	4.28 (0.92) ^e	2.14 (0.46) ^e	7.07 (1.52) ^e

Values in parentheses represent standard error of the mean. Values with different letters, within each parameter, were significantly different (Student-Newman-Keuls $P = 0.05$). The carbon stock values do not include woody debris or fine litter

and spatial pattern of root development of the species reported in this paper remains uncertain. Nonetheless, it was clear that the timing and proportion of total plant biomass allocated to roots and root bole did not increase significantly until years 4 and 5, and this appears to be related to the period (years after planting) that plants require to establish their root systems sufficiently to sustain an increase in growth rate. With the exception of the broadleaved and plate-rooted *Alectryon excelsus*, the tap-rooted and predominantly coniferous species allocated more of their total BGB to the root bole than did the remaining plate-rooted species or the tap-rooted *Agathis australis*. That said, there is also likely to be a relationship between plant size and the rate of root and root bole biomass accumulation with the smallest and slowest growing of the conifers *Agathis australis*, *Prumnopitys taxifolia* and *Prumnopitys ferruginea* amassing the least BGB.

Between years 1 and 3, there was no consistent relationship between the diameter of the canopy and root system dimensions (diameter) of tap- versus plate-rooted species or between conifer and broadleaved species. However, by year 4 and thereafter, the diameter of the root systems of the broadleaved *Alectryon excelsus* and *Vitex lucens* and the conifer *Dacrycarpus dacrydioides* exceeded the width of their respective canopies suggesting that the ratio of root spread to canopy dripline may be different for different species at the same age. From the few available descriptions of root system diameters of mature trees, it is evident that the lateral roots of conifers *Dacrydium cupressinum* and *Podocarpus totara* may extend > 9 m from the root bole (Bergin and Gea 2005, 2007). Similarly, the lateral roots of mature *Prumnopitys taxifolia* are often seen exposed on the ground surface and extending to > 19.5 m from the root bole before disappearing into the soil (Allan 1926), and thus, for the more conical-shaped conifers, their lateral roots likely extend beyond the canopy dripline.

The high concentration of roots (mass and length) of both the tap- and plate-rooted species at shallow depth was also anticipated. General observations of the root systems of mature plate-rooted indigenous species confirm that their root systems are largely confined to the uppermost metre or two of the soil with the prevalence of shallow rooting in forest soils likely reflecting dependence on nutrient cycling through litter fall (Yeates 1924; Cranwell and Moore 1936; Wardle 2002). Furthermore, observations of the root systems of the mature, plate-rooted *Dacrycarpus dacrydioides* indicate that their lateral structural roots are shallow and often sub-aerial as an adaptation to imperfectly drained soils and/or wetter flatland sites including alluvial floodplains and terraces with a periodic high water table dominated by pasture grasses (Wardle 2002). Alternatively, as suggested by Nicoll and Ray (1996), a shallow and extensive lateral root network may also be an adaptation to improve the rigidity of the soil-root plate and counteract the increasing vulnerability to windthrow as trees grow taller. Similarly, the development of an extensive network of lateral structural roots in *Populus* and *Salix* species makes them the preferred species for soil conservation and slope reinforcement on poorly drained sites such as earthflows (Phillips et al. 2014).

The maximum rooting depth recorded for an indigenous forest species is for a mature tap-rooted *Agathis australis*. Unless impeded by rock or a hard soil pan, tap roots have been recorded at depths in excess of 2 m (Bergin and Steward 2004), and 'sinker roots' have been observed to descend from large, lateral roots to a depth of 4 m and terminate in a network of smaller roots (R. LLoyd, pers. comm. cited in; Bergin and Steward 2004). *Agathis australis* is predominately found growing in the more sub-tropical regions of New Zealand so the early development of a deep tap root and relatively large biomass allocation to roots should be beneficial to surviving

droughts as suggested by Becker and Castillo (1990). It has also been suggested that a larger (and early) allocation to root biomass is beneficial for tree establishment (T Poulson, pers. comm. cited in Coutts 1987).

Biomass and carbon accumulation

Nationally, there is 1.45 Mha of marginal pastoral land suitable for reforestation by indigenous trees and shrubs (Trotter et al. 2005). The industry standard for establishment plantings of non-native species (principally *Pinus radiata*) on marginal land varies considerably depending on the class of land and its erosion severity (National Water and Soil Conservation Organisation 1976). In the highly erodible East Coast region of the North Island, the planting density is generally around 1000–1250 stems per hectare (spha). The establishment of a mixed indigenous forest comprising 125 of each of the eight species trialled here (1000 spha) would potentially amass $\sim 1.5 \text{ t ha}^{-1}$ within 5 years of planting, which would generate a forest carbon stock of $2.5 \text{ t CO}_2 \text{ ha}^{-1}$. With the exception of *Agathis australis*, the remainder of the conifers (mainly tap-rooted species) individually accumulated significantly more total plant biomass than did any of the plate-rooted species, while the broad-leaved *Vitex lucens* (also tap-rooted) accumulated the largest total biomass of any of the trialled species (Table 4, Additional file 3). Selection of a species mix comprising 200 of each of the best performing of the tap-rooted conifers (*Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Podocarpus totara*) and the broad-leaved *Vitex lucens*, together with the best performing of the plate-rooted broadleaved *Alectryon excelsa* would amass $\sim 2.3 \text{ t ha}^{-1}$, a forest carbon stock of $3.8 \text{ t CO}_2 \text{ ha}^{-1}$. Furthermore, an early colonising indigenous shrubland species mānuka (*Leptospermum scoparium* (Forster et Forster f.)) established at the same density would amass $\sim 3.7 \text{ t ha}^{-1}$ resulting in a forest carbon stock of $6.1 \text{ t CO}_2 \text{ ha}^{-1}$ over the same 5-year period (Marden and Lambie 2016). Thus, the planting of *Leptospermum scoparium* on marginal land would store an additional $\sim 2.3 \text{ t CO}_2 \text{ ha}^{-1}$ over an equivalent period of time than that gained from planting an equivalent density of the best performed of the trialled broadleaved and conifer species. Interestingly, the carbon stock for areas of indigenous forest 5 years after establishment (planting), or from the date when land-use change to reversion commences, is estimated at $7.8 \text{ t CO}_2 \text{ ha}^{-1}$ (Ministry for Primary industries 2017). By implication, to achieve a similar level of carbon stock within this time frame would for areas of new plantings require ~ 2000 spha of the best performed of the trialled broadleaved and conifer species. Similarly, for areas set aside to permit *passive* reversion to occur would require an equivalent density of mixed broadleaved and conifer

species, and for areas *actively* planted and managed for mānuka honey production, 1200–1300 spha would be required.

For the best performed of the trialled species, a monoculture of broadleaved *Vitex lucens* planted at 1000 spha could potentially achieve a level of forest carbon stock of $7.07 \text{ t CO}_2 \text{ ha}^{-1}$ by year 5 (Table 4), which approximated to the $7.8 \text{ t CO}_2 \text{ ha}^{-1}$ estimated by the Ministry for Primary Industries (2017) for new areas of planted and reverting shrubland. However, irrespective of the species mix and planting regime adopted for new areas of indigenous forest establishment, the potentially achievable forest carbon stock by year 5 is likely to be an order of magnitude less than the $\sim 91.6 \text{ t CO}_2 \text{ ha}^{-1}$ of forest carbon stock recorded for 4-year-old *Pinus radiata* (from Marden et al. 2016) and the $77 \text{ t CO}_2 \text{ ha}^{-1}$ estimated by the Ministry for Primary Industries (2017) for 5-year-old post-1989 plantings in the East Coast region.

Notwithstanding, the planting of indigenous conifers and broadleaved species on erodible marginal land will ultimately afford a more continuous and permanent forest sink for carbon over an active growth phase that extends from 150 to 500 years (Hall 2001; Hinds and Reid 1957) that is consistent with the prolonged effort likely required to effect significant reductions in atmospheric CO_2 levels.

Towards implementation

The second objective of this trial was to assess the potential effectiveness of the trialled species for erosion control on newly afforested/reforested marginal pastoral land and/or as replacement species best suited to providing long-term stability to areas of exotic forest deemed at greatest risk to storm-related erosion and under consideration for retirement in the future.

The well-developed literature on the geomechanical effects of vegetation on hill slope stability clearly indicate that tree roots reinforce soils, contribute to soil strength and stabilise eroding hillslopes. The mechanical interactions of woody roots with the soil medium play an important role in tree anchorage and thus in the prevention of slope failure. Thus, one of the most important traits is rooting depth, which, when soil conditions are not limiting, is species dependent. The most effective slope stabilisation results when root development occurs at different depths in the soil profile (Schiechl and Stern 1994; Czernin and Phillips 2005). This has been observed in exposed root boles of mature *Dacrydium cupressinum* and *Agathis australis*.

In New Zealand, shallow landslides on typically steep slopes underlain by Tertiary-aged bedrock are generally $\leq 1 \text{ m}$ deep (Marden et al. 1991; Page et al. 1994) so roots must cross the basal shear plane in order to anchor

the soil into more stable substrate and stabilise a slope against the initiation of shallow landslides (Wu et al. 1979). This study shows that, for most of the tree species examined, the root systems are concentrated predominantly in the upper soil profile with mean maximum root depths by year 5 ranging between 0.3 and 0.4 m. Furthermore, at this stage of their development, there was no significant difference in this metric among individual conifer species, between conifer and broadleaved species or between plate-rooted and tap-rooted species. The results also indicate that there is a rapid decline in roots with increasing depth and distance from the stem, that there are interspecies differences in root distribution and that each species allocates differing proportions of their total biomass to roots at different stages of growth, a finding similar to other local (Watson et al. 1995, 1999) and international (Abernethy and Rutherford 2001; Easson and Yarbrough 2002) studies on plant root distribution. This, together with the few published reports on the root depth of some of New Zealand's tallest native conifer and hardwood forest species (Cameron 1963), with the exception of *Agathis australis*, indicate that the rooting depth of mature trees rarely exceeded 2–3 m. By implication, their comparatively shallow rooting depth will likely be a limiting factor in their ability to contribute to deep-soil reinforcement. Similarly, the ability of widely spaced plantings to prevent the occurrence of shallow landslide diminishes as root distribution decreases with increasing distance from the root bole.

Interspecies differences in root distribution (depth and lateral spread) have implications for the planting densities required to provide full, near-surface root occupancy of the soil and/or to maximise the root density to the depth requirement at specific sites (Phillips et al. 2012). For example, a dense lateral network of woody roots predominantly confined to the upper soil horizons often forms a membrane that stabilises shallow soils (Schmidt et al. 2001) and significantly reduces shallow landslide potential on steep slopes (Ekanayake et al. 1997), while the larger tree roots can provide reinforcement across lateral planes of weakness bounding potential slope failures (Sidle et al. 1985). However, deeper soil mantles (>5 m) benefit little from such reinforcement as root density decreases dramatically with depth and few large roots are able to anchor across the basal shear plane (Stokes et al. 2008). The only benefit of root strength to the stabilisation of deep-seated landslides, e.g. earthflows and slumps, is when very large lateral woody roots cross planes of weakness along the flanks of potential failures (Sidle and Ochiai 2006). However, such reinforcement would only benefit deep-seated landslides of small area extent whereas lateral roots also offer protection against most shallow landslides (Swanston and Swanson 1976).

Larger diameter roots at greater soil depths would be desirable to stabilise the deeper forms of mass movement; thus, root diameter is another important consideration on landslide-prone slopes as thick roots reinforce soil in the same way that concrete is reinforced with steel rods, and the thicker the root, the greater its ability to penetrate soil (Clark et al. 2008). The most common barriers limiting the development of a deep rooting system include a permanent high water table, bedrock interface or a cemented iron pan and stoniness and depth of colluvium. In general terms, the root:shoot ratios of seedlings are depressed on such sites. As previously found for other New Zealand woody species, root depth was not necessarily correlated with tree age but rather to the stoniness and depth of slope colluvium (Watson et al. 1995).

In terms of root anchorage, tap-rooted species will, in time, likely provide a higher level of reinforcement directly under a tree and to a greater depth than for plate-rooted species. Thus, for tap-rooted species, root reinforcement quickly tapers off laterally as root density declines with increasing distance from the tree. In contrast, plate-rooted species with their widespread development of a lateral root network will likely provide a high level of near-surface soil-root reinforcement but nonetheless remain more susceptible to uprooting than will tap-rooted species because as the number of roots decline with increased depth (Gray and Sotir 1996) so does root anchorage rapidly decline (Dupuy et al. 2005; Norris et al. 2008).

As a consequence of their shallow-rooted habit, many of New Zealand's conifer and broadleaved trees will have limited effectiveness in floodplain reaches where channel hydraulic conditions are likely to result in the undercutting of stream banks to a depth greater than that of the maximum penetration depth of root systems (Marden et al. 2005). If the potential for streambed degradation exists, additional protection in the form of structural materials (e.g. gabion baskets and rip rap) will be required along the toe of banks and to some depth below normal streambed level. The limitations of root depth aside, some of the trialled conifer and broadleaved species have adaptations suitable for floodplain restoration. Alluvial communities of some of New Zealand's oldest podocarps (*Podocarpus totara*, *Dacrycarpus dacrydioides*) are tolerant of wet soils and swampy sites subjected to periodic flooding and seasonally high water tables. They have the ability to produce a new root system after flooding and inundation with river silt, and *Podocarpus totara* is able to produce tiers of adventitious roots from the buried part of the stem should the tree topple or break. *Dacrycarpus dacrydioides*, however, is intolerant of siltation if greater than ~60 cm (Foweraker 1929; McSweeney 1982; Campbell 1984). Many species, including *Dacrydium*

cupressinum, *Podocarpus totara* and *Agathis australis*, are equally tolerant of harsh growing conditions on steep slopes with skeletal soils deficient in nutrients that are prone to drying during seasonal droughts.

Although native conifers and broadleaved trees have not traditionally been used specifically for soil conservation, their successional role meets most of the requirements for use in revegetation where long-term erosion control is required (Pollock 1986). It is also important to consider that, in addition to its erosion-control function, a species mix may have greater associated ecological, cultural, aesthetic and economic benefits than a single species stand. In addition, most are sufficiently diverse in rooting form to stabilise slopes prone to shallow landslides and dry raveling, while those with the limitations of root depth will be less effective in stabilising the deeper forms of mass movements such as earthflows and slumps as their failure plane tends to be deeper than the vertical limit of root penetration. Plant density and species mix are also key factors in determining plant effectiveness; thus, options that promote the quickest canopy closure and root development at all levels of the soil profile are likely to be the most effective in promoting slope stability (Phillips et al. 2001). The faster the soil is occupied by roots, the greater the reinforcement of the soil and the greater the chance of limiting landslide initiation on erosion-prone slopes and dry raveling of exposed soil and rock. As an example, soil occupancy by the larger root systems of the broadleaved *Vitex lucens* and *Alectryon excelsus* would occur sooner (~5 years after planting) than the best performed of the conifers (*Podocarpus totara*) tested under optimal growth conditions and using the mean maximum root spread at year 5 as an indicator of the rate at which soil-root reinforcement might be considered as being effective against erosion. Conversely, the more compact root systems of *Prumnopitys taxifolia*, *Prumnopitys ferruginea* and *Dacrydium cupressinum* would take longer (~10–15 years) to be effective and the significantly smaller root system of *Agathis australis*, the longest. Phillips et al. (2015) compared the lateral root spread of exotic species including alder (*Alnus rubra*), cherry (*Prunus serrulatus*), blackwood (*Acacia melanoxylon*) and redwood (*Sequoia sempervirens*) with reported values for indigenous riparian species (Marden et al. 2005), for mānuka (Marden and Lambie 2016) and for *Pinus radiata* at a similar age (Watson and Tomblinson 2002, 2004; Marden et al. 2016). The conclusion drawn was that the species with the larger root system dimensions would provide earlier soil-root reinforcement and thus be more effective in mitigating the initiation of shallow landslides. Similarly, using root depth as an indicator of species potential for stabilising deeper-seated forms of erosion (e.g. rotational slumps and larger earthflows), tap-rooted

species (e.g. *Agathis australis*) have the potential to develop thicker and stronger roots able to penetrate across the basal shear plane to provide a deeper level of reinforcement, albeit only for the smaller deep-seated failures, than would plate-rooted species. Nonetheless, as was evident before the mature indigenous forest cover was removed from hill-country areas, given time to mature, these same species will slow down but may not completely arrest many of the deeper-seated forms of mass failure.

For many restoration sites, the strategy adopted should ideally include a mix of early colonising and successional species with plate- and tap-rooted characteristics. On less exposed sites, a mixture of shrub and tree species can be planted concurrently with the longer-lived conifer and broadleaved species interplanted at near final spacing (Bergin and Gea 2005, 2007). Another option that has found favour with many community groups is to restrict the number of colonising species (three or four) and then carry out follow-up planting with the late succession, longer-lived species after a few years to fill in any gaps created by failures from the initial planting (Fred Lichtwark pers. comm.).

During selection of suitable plant materials, the capacity of species to match specific site conditions, e.g. those that are long lived and can overcome potential limitations to successful establishment such as overcrowding resulting in suppressed growth (less is often best in the long term), frost, fungal and insect attack, browsing, wind throw and stem breakage, must also be taken into account. Potential limitations to a successful establishment outcome of the trialled species, particularly during the early growth period, include susceptibility to frost (e.g. *Alectryon excelsus*, *Vitex lucens*, *Dacrydium cupressinum*, *Agathis australis*), insect damage (e.g. *Podocarpus totara*, *Dacrydium cupressinum*, *Dacrydium dactyloides*, *Agathis australis*), fungi (e.g. *Agathis australis*, *Podocarpus totara*), browsing feral mammals (e.g. *Dacrydium cupressinum*, *Podocarpus totara*, *Agathis australis*) and stem snap (e.g. *Alectryon excelsus*) (Bergin and Gea 2005, 2007).

Conclusions

This study has provided much-needed new information on the overall growth performance of eight of New Zealand's more common conifer and broadleaved forest species. However, the conclusions drawn are primarily premised on their early growth period (first 5 years) at one trial site; thus, it must be acknowledged that allometric relationships will likely change with increasing tree age. The excavation of whole-plants has provided rare and valuable insights into inter-species differences in root architecture (dimensions), root sizes and biomass and their distribution relative to soil depth and distance

from the stem. Such data are integral to the selection of an appropriate species mix, planting density and as a means of assessing the period (years after planting) juvenile plantings are likely to remain vulnerable to the initiation of shallow landslides. Although the juvenile plants of the trialled species typically develop very shallow root systems, observations and anecdotal descriptions of the root systems of older trees show they have potential for mitigating shallow landslides, earthflows of small extent and dry raveling within a few years of planting. Conversely, as the basal failure plane of the deeper forms of mass movements such as earthflows and slumps tends to be deeper than the vertical limit of root penetration of the majority of the trialled species, their stabilisation will occur progressively over several decades.

The previously unavailable species-specific information on rates of whole-plant biomass accumulation for the indigenous forest species presented in this paper will improve current estimates of forest carbon stocks ($t\ CO_2\ ha^{-1}$) during the juvenile stage of growth of mixed-species or single-species woodlots proposed for new plantings on land considered marginal for pastoral use and unsustainable for short-rotation exotic forestry.

Species-specific growth performance data for both old-growth and juvenile trees of many of New Zealand's indigenous species remain elusive. It is therefore important that further time-series baseline data on plant growth rates are collected for a greater variety of New Zealand's indigenous species across a diversity of site conditions known to influence plant growth and that data on root metrics, in particular, are collected in a format suitable for inclusion in slope stability and/or soil reinforcement models (e.g. Schwarz et al. 2010), many of which suffer from a paucity of the types of data collected in this study (Phillips et al. 2012).

Endnotes

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Additional files

Additional file 1: Ecological and site requirements of the trialled species. (DOCX 16 kb)

Additional file 2: Mean above-ground attributes of six indigenous conifer and two broadleaved species. (DOCX 17 kb)

Additional file 3: Mean tree component biomass, above-ground (AGB) and below-ground (BGB) biomass totals and BGB/AGB ratio. (DOCX 23 kb)

Additional file 4: Mean below-ground attributes of six indigenous conifer and two broadleaved species. (DOCX 17 kb)

Additional file 5: Mean root and root bole biomass (g), as a percent of total below-ground biomass (BGB). (DOCX 19 kb)

Additional file 6: Mean root biomass (g) and percent of total root biomass, by 0.5-m radial increments from the root bole. (DOCX 19 kb)

Additional file 7: Mean and percent of total root length (m) of roots > 1 mm diameter, by 0.5-m radial increments from the root bole. (DOCX 23 kb)

Abbreviations

AGB: Above-ground biomass; AGS: Afforestation Grant Scheme; BGB: Below-ground biomass; BP: Before present; C: Carbon; CO_2 : Carbon dioxide; DBH: Diameter at breast height; ETS: Emissions Trading Scheme; FCCC: Framework Convention for Climate Change; GPR: Ground-penetrating radar; IPCC: Intergovernmental Panel on Climate Change; PFSI: Permanent Forest Sink Initiative; RCD: Root collar diameter; spha: Stems per hectare

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Availability of data and materials

Please contact the author for data requests.

Authors' contributions

MM was the primary author. MM, SL and CJP undertook the fieldwork. SL compiled the data into spreadsheets and completed the statistical analyses. All authors read and approved the manuscript.

Competing interests

The authors declare that they have no competing interests.

Ethics approval and consent to participate

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Additional file 1 Ecological and site requirements of the trialled species.

***Dacrydium cupressinum* (rimu)**

Found in lowland and montane forests it tolerates a wide range of soil types and soil moisture conditions and is found over a wide climatic range. Seedlings require shelter and flourish in well-lit forest gaps but persists in shade and can grow up to 50 m tall but more commonly 20–25 m with 1.5 m diameter. It is the least palatable of the native conifers, can be raised from cuttings, and once established is considered to be fast growing. Rootlets bear lateral nodules and there is grafting between the roots of the same and adjacent trees. Rimu competes with grasses better than most indigenous species, is relatively unpalatable to domestic stock but is browsed by possums.

***Podocarpus totara* (totara)**

Dominant in lowland and montane forests from sea level to 550 m totara prefers immature and not necessarily fertile, free-draining dry soils but is intolerant of poorly drained soils though can survive on sites subject to heavy silting. It tolerates wind, drought and is frost resistant, save for young seedlings, which are non-shade-tolerant.

Although a forest tree, it is well suited for growing in the open and is the most light-demanding of the conifers. Its growth becomes stagnant in shade or competition, but revives quickly when released. Totara is long lived and has moderate growth rates (11 m high and 23 cm diameter after 40 years). It has poor stem form in the open, is often multi-leadered if planted at low stocking, and at times can suffer from defoliation by insects and stem damage from cicada eggs, it is relatively unpalatable to domestic stock but is browsed by possums.

Prumnopitys ferruginea (miro)

Occurring in mixed lowland forests from sea level to 1000 m, miro is ubiquitous on infertile soils but extend to semi-fertile soils where moisture is adequate. Prefers well drained deep pumice soils but tolerates periodic wet soil conditions. Miro is one of the slower-growing conifers (up to 12 m high with 26 cm diameter in 60 years) with hard, durable wood.

Prumnopitys taxifolia (matai)

Matai is dominant in montane and lowland forests and tolerates a wide range of semi fertile, well drained, moist soils such as alluvium and pumice. It is one of the slower growing native conifers, (13 m high and 19 cm diameter after 60 years) for planted trees on a range of sites, and has heartwood that is durable above-ground but not ground durable.

Agathis australis (kauri)

Kauri grows in lowland and montane forests between sea level and 360 m with good growth rates on fertile colluvial and weathered volcanic soils but also tolerates infertile and ultra-infertile soils. It is one of the fastest growing native conifers (15 m high and 30 cm

diameter after 40 years). It is tolerant of periodic dry conditions hence survives on dry skeletal ridges but is intolerant of persistently wet sites. Its effective use of nutrients and water makes it suitable for poorer soil types. Kauri requires warm temperatures, relatively high light conditions and displays good growth on lower slopes where trees have survived competition from broadleaf species. The nodular rootlets of kauri are strongly mycotrophic. Planted kauri seems to grow better on moist, fertile soils than does naturally regenerated kauri and it performs best with weed control in early years following establishment.

***Dacrycarpus dacrydioides* (kahikatea)**

Kahikatea is the dominant species in swampy lowland and hilly forests between sea level to 700 m. It tolerates a wide range of soils from heavy clays to well drained pumice and alluvium thus grows best on wet ground but is intolerant of dry soils. Seedlings prefer full overhead light and shelter but tolerate shade and can grow to 60 m tall thriving best in forests but occasionally also in groves or as separate trees. Kahikatea is palatable to browsing animals and its brittle stems are subject to animal and wind damage. It has high survival and fast growth rates (14 m high and 27 cm diameter after 40 years) once established; however, its narrow and flexible stems are vulnerable to over-topping by dense re-growth of ferns, broadleaved species and vines (convolvulus) soon after planting. Its longevity and suitability for primary succession on wet heavy soils make it useful for long-term erosion control, although kahikatea does not tolerate heavy siltation. Defoliating by caterpillars, stick insects and browsing animals can result in tree mortality .

***Alectryon excelsus* (titoki)**

Titoki is a typical component of montane and lowland forests between sea level to 600 m. It tolerates a wide range of moisture conditions but prefers well-drained sites with associated lowland soils on fertile alluvial flats, is typically multi-stemmed and produces very hard timber. It is prone to wind damage, possum and stock browsing.

***Vitex lucens* (puriri)**

Puriri occurs in lowland and coastal forests in warm temperate areas on fertile, well-drained hill and floodplain alluvial soils where it grows up to 20 m high and 1.5 m in diameter. It tolerates a wide range of moisture conditions including summer drought but is prone to frost damage, possum and stock browsing. Puriri is one of the fastest growing native tree species in early years after establishment with annual increments in height of 40-50 cm and 1 cm in diameter. It coppices readily and its timber is black in colour, and dense, strong, and durable.

Additional file 2 Mean above-ground attributes of six indigenous conifer and two broadleaved species.

Botanical and common name and age	Height (m)	DBH (mm)	RCD (mm)	Canopy diameter (m)
Year 1				
<i>Agathis australis</i> (kauri)	0.19 (0.01) ^a	-	2.50 (0.17) ^{ab}	0.09 (0.004) ^a
<i>Dacrycarpus dacrydioide</i> (kahikatea)	0.41 (0.02) ^c	-	2.80 (0.13) ^{abcd}	0.15 (0.02) ^b
<i>Dacrydium cupressinum</i> (rimu)	0.38 (0.02) ^c	-	3.20 (0.13) ^{bd}	0.22 (0.02) ^c
<i>Podocarpus totara</i> (totara)	0.51 (0.02) ^d	-	3.90 (0.18) ^e	0.15 (0.01) ^b
<i>Prumnopitys ferruginea</i> (miro)	0.30 (0.02) ^b	-	2.10 (0.10) ^a	0.10 (0.01) ^a
<i>Prumnopitys taxifolia</i> (matai)	0.38 (0.02) ^c	-	2.78 (0.20) ^{abc}	0.13 (0.01) ^b
<i>Alectryon excelsus</i> (titoki)	0.20 (0.01) ^a	-	3.30 (0.15) ^d	0.14 (0.01) ^b
<i>Vitex lucens</i> (puriri)	0.30 (0.01) ^b	-	6.20 (0.20) ^f	0.19 (0.01) ^c
Year 2				
<i>Agathis australis</i> (kauri)	0.62 (0.06) ^b	-	9.20 (0.36) ^b	0.47 (0.03) ^c
<i>Dacrycarpus dacrydioide</i> (kahikatea)	0.84 (0.03) ^c	-	12.51 (0.5) ^c	0.29 (0.01) ^a
<i>Dacrydium cupressinum</i> (Rimu)	0.88 (0.04) ^c	-	8.90 (0.28) ^b	0.49 (0.02) ^c
<i>Podocarpus totara</i> (totara)	0.78 (0.05) ^{bc}	-	8.40 (0.37) ^b	0.41 (0.05) ^{bc}
<i>Prumnopitys ferruginea</i> (miro)	0.64 (0.02) ^b	-	5.20 (0.1) ^a	0.28 (0.02) ^a
<i>Prumnopitys taxifolia</i> (matai)	0.49 (0.02) ^a	-	5.20 (0.13) ^a	0.36 (0.05) ^{ab}
<i>Alectryon excelsus</i> (titoki)	0.92 (0.06) ^c	-	13.30 (0.63) ^c	0.32 (0.01) ^{ab}
<i>Vitex lucens</i> (puriri)	0.77 (0.03) ^c	-	15.40 (0.54) ^d	0.27 (0.02) ^a
Year 3				

<i>Agathis australis</i> (kauri)	0.97 (0.06) ^b	-	14.80 (0.63) ^{bc}	0.59 (0.03) ^b
<i>Dacrycarpus dacrydioide</i> (kahikatea)	1.25 (0.06) ^{cd}	-	17.05 (0.91) ^c	0.55 (0.01) ^b
<i>Dacrydium cupressinum</i> (rimu)	1.23 (0.04) ^{cd}	-	15.40 (0.86) ^{bc}	0.62 (0.05) ^b
<i>Podocarpus totara</i> (totara)	1.33 (0.07) ^d	-	14.40 (0.79) ^b	0.67 (0.06) ^b
<i>Prumnopitys ferruginea</i> (miro)	0.93 (0.02) ^b	-	9.10 (0.41) ^a	0.51 (0.03) ^b
<i>Prumnopitus taxifolia</i> (matai)	0.72 (0.02) ^a	-	10.04 (0.49) ^a	0.68 (0.04) ^b
<i>Alectryon excelsus</i> (titoki)	1.22 (0.04) ^{cd}	-	20.95 (1.18) ^d	0.56 (0.05) ^b
<i>Vitex lucens</i> (puriri)	1.19 (0.04) ^{bc}	-	22.70 (0.97) ^d	0.37 (0.02) ^a
Year 4				
<i>Agathis australis</i> (kauri)	1.19 (0.09) ^{ab}	1.70 (1.19) ^a	17.20 (1.14) ^a	0.55 (0.04) ^a
<i>Dacrycarpus dacrydioide</i> (kahikatea)	2.34 (0.11) ^f	9.08 (1.23) ^c	34.56 (1.74) ^b	0.98 (0.07) ^{bcd}
<i>Dacrydium cupressinum</i> (rimu)	1.89 (0.10) ^d	7.00 (0.99) ^{ac}	28.40 (0.70) ^b	1.07 (0.13) ^{cd}
<i>Podocarpus totara</i> (totara)	2.19 (0.10) ^{df}	10.20 (0.93) ^c	28.10 (1.52) ^b	1.25 (0.08) ^d
<i>Prumnopitys ferruginea</i> (miro)	1.32 (0.05) ^{bc}	0.90 (0.48) ^a	12.90 (0.55) ^a	0.72 (0.03) ^{ab}
<i>Prumnopitus taxifolia</i> (matai)	0.98 (0.06) ^a	-	17.70 (0.76) ^a	0.92 (0.06) ^{bc}
<i>Alectryon excelsus</i> (titoki)	1.92 (0.15) ^{de}	17.15 (4.05) ^d	32.00 (2.63) ^b	0.79 (0.08) ^{abc}
<i>Vitex lucens</i> (puriri)	1.53 (0.09) ^c	2.20 (1.44) ^{ab}	53.50 (6.11) ^c	1.40 (0.08) ^{cd}
Year 5				
<i>Agathis australis</i> (kauri)	1.55 (0.06) ^a	7.95 (1.73) ^{bc}	23.85 (0.98) ^a	0.80 (0.05) ^a
<i>Dacrycarpus dacrydioide</i> (kahikatea)	2.74 (0.16) ^c	16.84 (1.44) ^d	48.52 (2.65) ^c	1.05 (0.06) ^{abc}
<i>Dacrydium cupressinum</i> (rimu)	2.21 (0.06) ^b	9.80 (0.59) ^c	37.80 (1.36) ^b	1.34 (0.07) ^c

<i>Podocarpus totara</i> (totara)	2.82 (0.12) ^c	21.50 (1.79) ^d	49.90 (2.73) ^c	2.20 (0.10) ^e
<i>Prumnopitys ferruginea</i> (miro)	1.56 (0.06) ^a	2.75 (0.78) ^{ab}	19.90 (2.05) ^a	1.14 (0.07) ^{bc}
<i>Prumnopitys taxifolia</i> (matai)	1.31 (0.07) ^a	0.04 (0.27) ^a	23.90 (1.10) ^a	1.24 (0.05) ^b
<i>Alectryon excelsus</i> (titoki)	2.24 (0.10) ^b	9.97 (1.85) ^c	39.51 (2.70) ^b	1.03 (0.06) ^b
<i>Vitex lucens</i> (puriri)	2.39 (0.37) ^b	18.80 (7.74) ^d	77.60 (11.72) ^d	1.56 (0.24) ^d

Values in the brackets represent standard error of the mean. Values with different letters, within each parameter within each year, were significantly different (Student-Newman-Keuls $P = 0.05$). In year-1 there were no roots >1 mm diameter. Plants did not reach DBH height until year 4.

Additional file 3 Mean tree component biomass, above-ground (AGB) and below-ground (BGB) biomass totals, and AGB/BGB ratios.

Botanical & common name and age	Foliage (g)	Branches (g)	Stem (g)	Total AGB (g)	Total BGB (g)	BGB/AGB ratio
Year 1						
<i>Agathis australis</i> (kauri)	0.34 (0.03) ^{bc}	0.10 (0.00) ^a	0.16 (0.03) ^a	0.60 (0.04) ^a	0.20 (0.00) ^a	0.35 (0.03) ^{ab}
<i>Dacrycarpus dacrydioides</i> (kahikatea)	0.18 (0.02) ^a	0.26 (0.04) ^b	0.62 (0.05) ^d	1.06 (0.05) ^{abc}	0.33 (0.02) ^b	0.33 (0.03) ^{abc}
<i>Dacrydium cupressinum</i> (rimu)	0.35 (0.08) ^{bc}	1.16 (0.14) ^e	0.96 (0.07) ^e	2.47 (0.27) ^d	0.85 (0.09) ^d	0.35 (0.01) ^{ab}
<i>Podocarpus totara</i> (totara)	2.07 (0.08) ^e	0.41 (0.04) ^c	1.80 (0.11) ^f	4.28 (0.20) ^e	1.91 (0.17) ^e	0.44 (0.03) ^b
<i>Prumnopitys ferruginea</i> (miro)	0.45 (0.05) ^c	0.12 (0.01) ^a	0.41 (0.04) ^c	0.98 (0.10) ^{ab}	0.52 (0.04) ^c	0.55 (0.04) ^d
<i>Prumnopitys taxifolia</i> (matai)	0.28 (0.05) ^{ab}	0.87 (0.16) ^d	0.70 (0.05) ^d	1.95 (0.23) ^{bd}	0.51 (0.06) ^c	0.28 (0.03) ^a
<i>Alectryon excelsus</i> (titoki)	0.65 (0.07) ^d	0.10 (0.00) ^a	0.28 (0.03) ^b	1.03 (0.07) ^{abc}	0.31 (0.03) ^b	0.30 (0.02) ^a
<i>Vitex lucens</i> (puriri)	2.26 (0.28) ^e	0.33 (0.05) ^{bc}	1.76 (0.21) ^f	4.35 (0.51) ^e	3.84 (0.42) ^f	0.89 (0.04) ^e
Year 2						
<i>Agathis australis</i> (kauri)	10.57 (0.68) ^e	4.92 (0.54) ^b	8.09 (0.50) ^c	23.57 (1.62) ^{bc}	3.85 (0.40) ^a	0.16 (0.01) ^a
<i>Dacrycarpus</i>	9.43 (0.74) ^{de}	6.85 (0.67) ^b	14.02 (1.30) ^d	30.30 (2.50) ^d	9.73 (1.09) ^c	0.32 (0.01) ^{bc}

<i>dacrydioide</i> (kahikatea)						
<i>Dacrydium cupressinum</i> (rimu)	7.48 (0.07) ^{cd}	15.48 (1.67) ^c	9.38 (0.61) ^c	32.70 (2.75) ^d	7.72 (0.82) ^{bc}	0.23 (0.01) ^b
<i>Podocarpus totara</i> (totara)	6.91 (0.60) ^c	5.17 (0.96) ^b	7.99 (0.42) ^c	20.07 (1.57) ^b	6.07 (0.45) ^b	0.31 (0.01) ^c
<i>Prumnopitys ferruginea</i> (miro)	3.55 (0.15) ^b	2.11 (0.18) ^a	3.29 (0.19) ^b	8.95 (0.51) ^a	4.18 (0.29) ^a	0.47 (0.02) ^e
<i>Prumnopitys taxifolia</i> (matai)	1.23 (0.68) ^a	5.87 (0.39) ^b	2.33 (0.19) ^a	9.43 (0.67) ^a	3.41 (0.23) ^a	0.36 (0.02) ^{cd}
<i>Alectryon excelsus</i> (titoki)	17.16 (1.26) ^f	7.20 (1.07) ^b	21.77 (3.39) ^e	46.13 (4.45) ^e	19.24 (2.35) ^d	0.42 (0.04) ^{de}
<i>Vitex lucens</i> (puriri)	10.84 (0.44) ^e	2.27 (0.12) ^a	17.92 (0.75) ^e	31.03 (0.91) ^{cd}	14.63 (1.07) ^d	0.48 (0.04) ^e
Year 3						
<i>Agathis australis</i> (kauri)	25.23 (2.98) ^{bcd}	12.95 (1.48) ^{ab}	28.98 (3.39) ^b	67.16 (7.58) ^a	17.18 (1.61) ^a	0.28 (0.04) ^a
<i>Dacrycarpus dacrydioide</i> (kahikatea)	16.08 (1.76) ^{abc}	22.05 (2.88) ^{bcd}	33.19 (4.57) ^b	71.32 (8.97) ^{ab}	33.34 (4.09) ^{bc}	0.47 (0.02) ^{bc}
<i>Dacrydium cupressinum</i> (rimu)	27.77 (5.39) ^{bcd}	61.29 (7.01) ^a	37.10 (3.55) ^b	124.83 (15.22) ^b	34.69 (4.13) ^{bc}	0.29 (0.03) ^a
<i>Podocarpus totara</i> (totara)	34.04 (3.69) ^{bd}	22.10 (3.81) ^{bc}	25.65 (2.63) ^b	81.79 (8.65) ^{ab}	24.62 (2.49) ^{ab}	0.31 (0.02) ^a
<i>Prumnopitys ferruginea</i>	16.37 (1.97) ^b	12.43 (1.82) ^{ab}	16.96 (1.79) ^a	45.76 (5.21) ^a	16.86 (1.49) ^a	0.38 (0.02) ^{ab}

(miro)						
<i>Prumnopitys taxifolia</i> (matai)	9.06 (1.05) ^a	37.61 (6.34) ^{ce}	13.98 (1.15) ^a	60.65 (8.22) ^a	17.84 (1.86) ^a	0.31 (0.02) ^a
<i>Alectryon excelsus</i> (titoki)	76.59 (15.19) ^e	46.24 (7.86) ^e	87.66 (10.65) ^c	210.49 (31.34) ^c	100.65 (12.21) ^d	0.51 (0.03) ^c
<i>Vitex lucens</i> (puriri)	29.33 (6.74) ^{bcd}	10.85 (2.07) ^a	63.52 (6.34) ^c	103.70 (12.87) ^{ab}	43.92 (5.89) ^c	0.44 (0.04) ^{bc}
Year 4						
<i>Agathis australis</i> (kauri)	37.59 (4.89) ^a	18.93 (2.49) ^a	54.87 (7.67) ^a	106.14 (13.57) ^a	27.48 (3.45) ^a	0.26 (0.01) ^b
<i>Dacrycarpus dacrydioides</i> (kahikatea)	132.69 (16.01) ^b	180.52 (24.36) ^{cd}	223.86 (26.09) ^{bc}	537.07 (64.07) ^b	212.59 (18.21) ^{de}	0.41 (0.02) ^c
<i>Dacrydium cupressinum</i> (rimu)	274.10 (41.55) ^c	101.54 (7.90) ^c	173.15 (18.28) ^b	548.83 (63.28) ^b	160.51 (13.81) ^d	0.30 (0.02) ^b
<i>Podocarpus totara</i> (totara)	205.20 (21.21) ^{bc}	199.36 (19.25) ^{cd}	201.57 (14.89) ^{bc}	606.13 (25.49) ^b	111.13 (9.45) ^e	0.18 (0.02) ^a
<i>Prumnopitys ferruginea</i> (miro)	43.49 (4.94) ^a	40.27 (5.74) ^b	51.85 (4.11) ^a	135.61 (14.21) ^a	52.44 (3.47) ^b	0.40 (0.02) ^c
<i>Prumnopitys taxifolia</i> (matai)	34.21 (4.35) ^a	174.42 (22.67) ^{cd}	47.21 (5.86) ^a	255.84 (30.89) ^a	76.92 (9.17) ^b	0.31 (0.02) ^b
<i>Alectryon excelsus</i> (titoki)	188.62 (38.98) ^b	252.75 (63.70) ^{cd}	393.82 (81.21) ^c	835.19 (176.79) ^c	333.83 (65.63) ^{ef}	0.44 (0.03) ^c
<i>Vitex lucens</i> (puriri)	326.42 (44.99) ^c	272.22 (51.48) ^d	313.22 (46.80) ^c	911.65 (133.88) ^c	363.13 (45.14) ^f	0.40 (0.02) ^c
Year 5						

<i>Agathis australis</i> (kauri)	81.48 (8.95) ^a	45.90 (5.98) ^a	123.70 (10.20) ^a	251.08 (24.36) ^a	71.99 (7.97) ^a	0.30 (0.02) ^{ac}
<i>Dacrycarpus dacrydioide</i> (kahikatea)	297.21 (49.78) ^b	430.94 (77.72) ^{cde}	502.99 (71.03) ^{bc}	1231.14 (193.10) ^b	371.25 (49.64) ^c	0.32 (0.02) ^{cd}
<i>Dacrydium cupressinum</i> (rimu)	592.72 (46.16) ^c	234.42 (33.13) ^c	338.05 (22.51) ^b	1165.19 (84.04) ^b	397.39 (46.16) ^c	0.33 (0.02) ^{cd}
<i>Podocarpus totara</i> (totara)	718.08 (81.09) ^c	789.38 (169.25) ^{def}	635.48 (66.37) ^{cd}	2142.94 (290.35) ^c	449.96 (45.37) ^c	0.23 (0.02) ^a
<i>Prumnopitys ferruginea</i> (miro)	121.97 (20.71) ^a	127.36 (24.15) ^b	132.05 (22.92) ^a	381.38 (65.16) ^a	134.87 (23.62) ^b	0.35 (0.01) ^{cd}
<i>Prumnopitys taxifolia</i> (matai)	81.54 (10.40) ^a	401.18 (42.56) ^{cde}	98.25 (9.37) ^a	580.97 (56.85) ^{ab}	134.59 (13.99) ^b	0.23 (0.01) ^{ab}
<i>Alectryon excelsus</i> (titoki)	216.30 (25.58) ^b	437.72 (98.67) ^{cd}	438.34 (84.68) ^{bc}	1092.37 (183.20) ^b	402.16 (52.87) ^c	0.38 (0.02) ^{de}
<i>Vitex lucens</i> (puriri)	934.52 (222.22) ^c	1037.76 (278.30) ^{df}	1053.74 (238.79) ^d	3026.02 (653.63) ^d	1257.38 (275.91) ^d	0.41 (0.02) ^e

Values in the brackets represent standard error of the mean. Values with different letters in each year and within each column were significantly different and P values in bold were significantly different (Student-Newman-Keuls $P = 0.05$).

Additional file 4 Mean below-ground attributes of six indigenous conifer and two broadleaved species.

Botanical and common name and age Year 1	Mean max. root spread (diameter m)	Mean total length (m) of roots >1 mm diameter	Mean max. root depth (m)
<i>Agathis australis</i> (kauri)	0.06 (0.004) ^a	-	0.09 (0.01) ^{abc}
<i>Dacrycarpus dacrydioide</i> (kahikatea)	0.07 (0.004) ^{ab}	-	0.08 (0.003) ^a
<i>Dacrydium cupressinum</i> (rimu)	0.09 (0.01) ^b	-	0.11 (0.01) ^{bc}
<i>Podocarpus totara</i> (totara)	0.11 (0.01) ^c	-	0.11 (0.01) ^{bc}
<i>Prumnopitys ferruginea</i> (miro)	0.08 (0.01) ^{ab}	-	0.09 (0.002) ^{abc}
<i>Prumnopitus taxifolia</i> (matai)	0.07 (0.01) ^{ab}	-	0.09 (0.005) ^{ab}
<i>Alectryon excelsus</i> (titoki)	0.07 (0.003) ^{ab}	-	0.11 (0.01) ^c
<i>Vitex lucens</i> (puriri)	0.13 (0.01) ^c	-	0.10 (0.002) ^{abc}
Year 2			
<i>Agathis australis</i> (kauri)	0.11 (0.01) ^a	0.41 (0.07) ^a	0.11 (0.004) ^b
<i>Dacrycarpus dacrydioide</i> (kahikatea)	0.14 (0.004) ^{ab}	2.07 (0.26) ^c	0.17 (0.01) ^d
<i>Dacrydium cupressinum</i> (Rimu)	0.15 (0.002) ^{ab}	1.22 (0.14) ^a	0.14 (0.01) ^c
<i>Podocarpus totara</i> (totara)	0.15 (0.003) ^{ab}	0.95 (0.10) ^{ab}	0.09 (0.01) ^a
<i>Prumnopitys ferruginea</i> (miro)	0.14 (0.003) ^{ab}	0.87 (0.13) ^{ab}	0.11 (0.004) ^b
<i>Prumnopitus taxifolia</i> (matai)	0.14 (0.002) ^{ab}	0.88 (0.06) ^{ab}	0.13 (0.002) ^{bc}
<i>Alectryon excelsus</i> (titoki)	0.18 (0.003) ^b	2.76 (0.28) ^d	0.12 (0.01) ^b
<i>Vitex lucens</i> (puriri)	0.15 (0.01) ^{ab}	2.91 (0.34) ^d	0.21 (0.01) ^e
Year 3			
<i>Agathis australis</i>	0.36 (0.04) ^a	2.62 (0.44) ^a	0.26 (0.01) ^a

(kauri)			
<i>Dacrycarpus dacrydioide</i>	0.67 (0.04) ^c	14.13 (2.07) ^b	0.1 (0.01) ^a
(kahikatea)			
<i>Dacrydium cupressinum</i>	0.53 (0.05) ^{abc}	7.30 (1.09) ^a	0.22 (0.02) ^a
(rimu)			
<i>Podocarpus totara</i>	0.61 (0.07) ^{bc}	4.84 (1.65) ^a	0.20 (0.01) ^a
(totara)			
<i>Prumnopitys ferruginea</i>	0.52 (0.03) ^{abc}	4.41 (0.45) ^a	0.24 (0.01) ^a
(miro)			
<i>Prumnopitus taxifolia</i>	0.47 (0.05) ^{ab}	2.96 (0.34) ^a	0.23 (0.01) ^a
(matai)			
<i>Alectryon excelsus</i>	0.98 (0.06) ^d	21.56 (3.37) ^c	0.19 (0.03) ^a
(titoki)			
<i>Vitex lucens</i>	0.87 (0.04) ^d	14.24 (1.79) ^b	0.19 (0.03) ^a
(puriri)			
Year 4			
<i>Agathis australis</i>	0.51 (0.04) ^a	4.53 (0.49) ^a	0.23 (0.02) ^{ab}
(kauri)			
<i>Dacrycarpus dacrydioide</i>	1.50 (0.09) ^c	89.24 (9.79) ^d	0.27 (0.01) ^{ab}
(kahikatea)			
<i>Dacrydium cupressinum</i>	0.95 (0.03) ^b	33.17 (2.91) ^b	0.27 (0.02) ^{ab}
(rimu)			
<i>Podocarpus totara</i>	1.14 (0.12) ^b	24.11 (0.89) ^{ab}	0.32 (0.08) ^b
(totara)			
<i>Prumnopitys ferruginea</i>	0.93 (0.03) ^b	12.56 (0.89) ^{ab}	0.18 (0.01) ^a
(miro)			
<i>Prumnopitus taxifolia</i>	1.03 (0.03) ^b	19.42 (1.88) ^{ab}	0.17 (0.02) ^a
(matai)			
<i>Alectryon excelsus</i>	1.71 (0.16) ^c	64.49 (10.41) ^c	0.20 (0.02) ^{ab}
(titoki)			
<i>Vitex lucens</i>	2.13 (0.11) ^d	97.70 (7.99) ^d	0.28 (0.02) ^{ab}
(puriri)			
Year 5			
<i>Agathis australis</i>	0.52 (0.03) ^a	9.01 (1.05) ^a	0.36 (0.06) ^a
(kauri)			
<i>Dacrycarpus dacrydioide</i>	1.71 (0.13) ^c	104.71(13.98) ^{bc}	0.30 (0.03) ^a
(kahikatea)			
<i>Dacrydium cupressinum</i>	1.13 (0.05) ^b	59.25 (9.55) ^{ab}	0.38 (0.01) ^a
(rimu)			
<i>Podocarpus totara</i>	2.23 (0.15) ^d	117.01 (18.89) ^c	0.37 (0.02) ^a

(totara)			
<i>Prumnopitys ferruginea</i>	0.98 (0.05) ^b	23.87 (3.59) ^a	0.26 (0.02) ^a
(miro)			
<i>Prumnopitys taxifolia</i>	1.15 (0.05) ^b	31.16 (3.82) ^a	0.29 (0.02) ^a
(matai)			
<i>Alectryon excelsus</i>	1.64 (0.10) ^c	92.93 (10.64) ^{bc}	0.25 (0.02) ^a
(titoki)			
<i>Vitex lucens</i>	2.54 (0.16) ^c	347.45 (75.34) ^d	0.34 (0.07) ^a
(puriri)			

Note. Values in brackets represent the standard error of the mean. Values with different letters, within each parameter within each year were significantly different (Student-Newman-Keuls $P = 0.05$).

Additional file 5 Mean root and root bole biomass (g), as a percent of total below-ground biomass (BGB).

Biomass type	Year 1		Year 2		Year 3		Year 4		Year 5	
	Biomass (g)	% of BGB	Biomass (g)	% of BGB	Biomass (g)	% of BGB	Biomass (g)	% of BGB	Biomass (g)	% of BGB
Root bole										
<i>Agathis australis</i> (kauri)	0.1 (0.00) ^a	50.0 (0.0) ^f	1.4 (0.2) ^{cd}	36.8 (5.5) ^c	4.1 (0.6) ^{ab}	23.6 (2.1) ^b	7.7 (1.0) ^a	29.9 (3.2) ^b	17.2 (1.7) ^a	24.8 (2.0) ^{bc}
<i>Dacrycarpus dacrydiode</i> (kahikatea)	0.1 (0.00) ^a	31.2 (1.5) ^d	1.9 (0.3) ^d	19.8 (1.8) ^{ab}	6.3 (1.3) ^{bc}	19.2 (3.1) ^{ab}	52.9 (6.6) ^c	24.1 (1.2) ^{bcd}	112.7 (17.3) ^{bc}	30.5 (1.8) ^c
<i>Dacrydium cupressinum</i> (rimu)	0.2 (0.03) ^a	16.5 (1.4) ^b	1.1 (0.2) ^c	14.7 (2.6) ^a	8.2 (1.3) ^{cd}	22.9 (2.9) ^b	42.1 (4.6) ^c	26.6 (2.3) ^{bc}	102.6 (10.9) ^b	26.6 (1.8) ^{bc}
<i>Podocarpus totara</i> (totara)	0.2 (0.03) ^a	9.1 (1.6) ^a	0.8 (0.1) ^{bc}	13.4 (1.0) ^a	3.8 (0.5) ^{ab}	14.8 (1.1) ^a	26.6 (4.0) ^b	24.5 (3.2) ^{bcd}	103.0 (9.5) ^{bc}	24.2 (2.5) ^{bc}
<i>Prumnopitys ferruginea</i> (miro)	0.1 (0.00) ^a	20.5 (1.9) ^{bc}	0.6 (0.1) ^{ab}	13.9 (1.2) ^a	2.3 (0.3) ^a	13.4 (1.0) ^a	7.3 (0.7) ^a	13.9 (0.8) ^a	22.2 (4.6) ^a	15.8 (1.5) ^a
<i>Prumnopitys taxifolia</i> (matai)	0.1 (0.00) ^a	24.0 (2.0) ^c	0.4 (0.1) ^a	12.7 (1.4) ^a	2.7 (0.5) ^a	14.8 (1.4) ^a	11.9 (1.5) ^a	16.0 (1.9) ^{ab}	22.9 (2.6) ^a	17.5 (1.4) ^a
<i>Alectryon excelsus</i> (titoki)	0.1 (0.00) ^a	42.3 (2.6) ^a	5.4 (1.0) ^e	27.0 (2.9) ^b	22.3 (3.2) ^e	22.9 (2.1) ^b	75.0 (23.5) ^c	21.8 (2.8) ^{abcd}	105.8 (14.8) ^{bc}	26.8 (2.3) ^{bc}
<i>Vitex lucens</i> (puriri)	0.4 (0.08) ^b	8.3 (1.3) ^a	3.8 (0.4) ^e	25.7 (2.1) ^b	10.2 (1.0) ^d	24.4 (1.7) ^b	73.0 (9.0) ^c	20.4 (1.1) ^{abc}	287.3 (81.3) ^b	20.7 (3.7) ^{ab}
Roots										
<i>Agathis australis</i> (kauri)	0.1 (0.00) ^a	50.0 (0.0) ^a	2.5 (0.4) ^a	63.2 (5.5) ^a	13.1 (1.3) ^a	76.4 (2.1) ^a	19.8 (12.7) ^a	70.1(3.2) ^a	54.8 (6.8) ^a	75.2 (2.0) ^{ab}
<i>Dacrycarpus dacrydiode</i> (kahikatea)	0.2 (0.02) ^b	68.8 (1.5) ^c	7.8 (0.9) ^d	80.2 (1.8) ^{bc}	27.0 (3.4) ^c	80.8 (3.1) ^{ab}	159.7 (12.1) ^{ef}	75.9 (1.2) ^{abc}	258.5 (34.3) ^c	69.5 (1.8) ^a
<i>Dacrydium cupressinum</i> (rimu)	0.7 (0.08) ^d	83.5 (1.4) ^e	6.6 (0.7) ^{cd}	85.4 (2.6) ^c	26.5 (3.4) ^c	77.1 (2.9) ^a	118.4 (11.5) ^{de}	73.4 (2.3) ^{ab}	294.8 (37.8) ^c	73.5 (1.8) ^{ab}
<i>Podocarpus totara</i> (totara)	1.8 (0.07) ^e	90.9 (1.6) ^f	5.2 (0.4) ^c	86.6 (1.0) ^c	20.8 (2.0) ^{bc}	85.2 (1.1) ^b	84.5 (8.0) ^{ef}	75.5 (3.2) ^{abc}	346.9 (41.3) ^c	75.8 (2.5) ^{ab}
<i>Prumnopitys ferruginea</i> (miro)	0.4 (0.04) ^c	79.5 (1.9) ^{de}	3.6 (0.3) ^b	86.1 (1.2) ^c	14.5 (1.2) ^{ab}	86.6 (1.0) ^b	45.1 (3.0) ^b	86.1 (0.8) ^d	112.7 (19.6) ^b	84.2 (1.5) ^c
<i>Prumnopitys taxifolia</i> (matai)	0.4 (0.05) ^c	76.0 (2.0) ^d	3.0 (0.2) ^{ab}	87.3 (1.4) ^c	15.2 (1.5) ^{ab}	85.2 (1.4) ^b	65.1 (8.4) ^{bc}	84.1 (1.9) ^{cd}	111.7 (12.4) ^b	82.5 (1.4) ^c
<i>Alectryon excelsus</i> (titoki)	0.2 (0.02) ^b	57.7 (2.6) ^b	13.9 (1.7) ^e	73.0 (2.9) ^b	78.3 (10.4) ^d	77.1 (2.1) ^a	258.8 (46.2) ^{fg}	78.2 (2.8) ^{abcd}	296.4 (40.1) ^c	73.2 (2.3) ^{ab}
<i>Vitex lucens</i> (puriri)	3.5 (0.35) ^f	91.7 (1.3) ^f	10.9 (0.8) ^e	74.4 (2.1) ^b	33.7 (5.1) ^c	75.6 (1.7) ^a	290.2 (37.6) ^g	79.6 (1.1) ^{bcd}	970.1 (209.6) ^d	79.3 (3.7) ^{bc}

Note: All (100%) of the root biomass for all species, and in each year of the trial, was confined to within the 0–0.5-m soil depth interval. Values in brackets represent the standard error of the mean. Values with different letters, within each parameter within each year, were significantly different (Student-Newman-Keuls ($P = 0.05$)).

<i>excelsus</i>								
(titoki)								
<i>Vitex lucens</i>	232.1 (38.8) ^f	92.1 (1.9) ^b	25.8 (8.1) ^a	7.7 (1.8) ^a	0.9 (0.6) ^a	0.2 (0.1) ^a		
(puriri)								
Year 5							-	-
<i>Agathis australis</i>	229.7 (29.0) ^f	79.9 (2.8) ^a	54.3 (9.8) ^b	18.4 (12.2) ^b	5.6 (2.6) ^b	1.7 (0.7) ^b		-
(kauri)							-	-
<i>Dacrycarpus dacrydioides</i>							-	
(kahikatea)	54.8 (6.8) ^a	100 (0.0) ^d	-	-	-	-		-
<i>Dacrydium cupressinum</i>							-	
(rimu)	226.9 (26.0) ^c	89.9 (9.0) ^c	31.1 (10.7) ^b	10.0 (2.7) ^b	0.6 (0.6) ^a	0.1 (0.1) ^a		-
<i>Podocarpus totara</i>							-	-
(totara)	291.7 (36.9) ^c	99.1 (0.5) ^d	3.2 (2.2) ^a	0.9 (0.5) ^a	-	-	-	-
<i>Prumnopitys ferruginea</i>								
(miro)	256.4 (24.0)	76.8 (3.2) ^b	78.7 (14.4) ^c	20.6 (2.6) ^c	11.9 (4.8) ^b	2.6 (0.9) ^b		
<i>Prumnopitys taxifolia</i>								
(matai)								
<i>Alectryon</i>	110.5 (19.0) ^b	98.4 (1.1) ^d	2.2 (1.7) ^a	1.6 (1.1) ^a	-	-		

<i>excelsus</i>								
(titoki)								
<i>Vitex lucens</i>	108.4 (11.4) ^b	97.6 (0.9) ^d	3.3 (1.5) ^a	2.4 (0.9) ^a	-	-		
(puriri)								
	265.6 (33.8) ^c	90.4 (8.4) ^c	30.8 (7.9) ^b	9.6 (1.8) ^b	-	-		-
	611.6 (134.2) ^d	65.9 (4.7) ^a	248.9 (64.4) ^d	23.1 (3.1) ^c	101.3 (36.1) ^c	10.3 (3.3) ^c	8.3 (5.5)	0.8 (0.6)

Note. In years 1–3, for each species all the root mass was confined to within a 0–0.5 m radius of the root bole. Values in brackets are representative of the standard error of the mean. Values with a different letter, within each year and within each radial segment were significantly different (Student-Newman-Keuls $P = 0.05$).

Additional file 7 Mean, and percent of total root length (m) of roots >1 mm diameter by 0.5 m radial increments from the root bole.

Botanical and common name and radial distance from root bole	Year 2		Year 3		Year 4		Year 5	
	Mean total root length	% of total root length	Mean total root length	% of total root length	Mean total root length	% of total root length	Mean total root length	% of total root length
0–0.5 m								
<i>Agathis australis</i> (kauri)	0.41 (0.07) ^a	100.00 (0.0)	2.62 (0.44) ^a	100.00 (0.0)	4.53 (0.49) ^a	100.00 (0.0) ^c	9.01 (1.05) ^a	100.00 (0.0) ^d
<i>Dacrycarpus dacrydioide</i> (kahikatea)	2.07 (0.26) ^c	100.00 (0.0)	14.13 (2.07) ^b	100.00 (0.0)	70.52 (7.77) ^e	79.72 (2.84) ^b	79.80 (8.08) ^{cd}	70.32 (5.39) ^c
<i>Dacrydium cupressinum</i> (rimu)	1.22 (0.14) ^a	100.00 (0.0)	7.30 (1.09) ^a	100.00 (0.0)	33.17 (2.91) ^c	100.00 (0.0) ^c	56.88 (8.44) ^c	96.93 (1.36) ^d
<i>Podocarpus totara</i> (totara)	0.95 (0.10) ^{ab}	100.00 (0.0)	4.84 (1.65) ^a	100.00 (0.0)	24.11 (0.89) ^{bc}	100.00 (0.0) ^c	67.55 (8.67) ^c	63.51 (4.91) ^b
<i>Prumnopitys ferruginea</i> (miro)	0.87 (0.13) ^{ab}	100.00 (0.0)	4.41 (0.45) ^a	100.00 (0.0)	12.56 (0.89) ^{ab}	100.00 (0.0) ^c	23.01 (3.29) ^b	97.22 (1.89) ^d
<i>Prumnopitys taxifolia</i> (matai)	0.88 (0.06) ^{ab}	100.00 (0.0)	2.96 (0.34) ^a	100.00 (0.0)	19.42 (1.88) ^{bc}	100.00 (0.0) ^c	28.23 (3.22) ^b	92.39 (3.12) ^d
<i>Alectryon excelsus</i> (titoki)	2.76 (0.28) ^d	100.00 (0.0)	21.56 (3.37) ^c	100.00 (0.0)	50.08 (6.36) ^d	82.57 (3.84) ^b	67.83 (4.77) ^{cd}	75.74 (4.36) ^c
<i>Vitex lucens</i> (puriri)	2.91 (0.34) ^d	100.00 (0.0)	14.24 (1.79) ^b	100.00 (0.0)	58.83 (6.56) ^{de}	60.13 (4.12) ^a	112.40 (24.46) ^d	36.68 (9.01) ^a
0.5–1.0 m								
<i>Agathis australis</i> (kauri)	-	-	-	-	-	-	-	-
<i>Dacrycarpus dacrydioide</i> (kahikatea)	-	-	-	-	17.35 (2.71) ^a	19.12 (2.50) ^a	24.34 (8.59) ^b	19.36 (5.33) ^b

<i>Dacrydium cupressinum</i> (rimu)	-	-	-	-	-	-	2.37 (1.58) ^a	3.07 (1.36) ^a
<i>Podocarpus totara</i> (totara)	-	-	-	-	-	-	39.53 (6.58) ^b	29.88 (3.60) ^{bc}
<i>Prumnopitys ferruginea</i> (miro)	-	-	-	-	-	-	0.92 (0.70) ^a	2.78 (1.89) ^a
<i>Prumnopitys taxifolia</i> (matai)	-	-	-	-	-	-	2.93 (1.46) ^a	7.61 (3.21) ^a
<i>Alectryon excelsus</i> (titoki)	-	-	-	-	14.01 (4.57) ^a	17.00 (3.70) ^a	25.10 (6.94) ^b	24.26 (4.36) ^b
<i>Vitex lucens</i> (puriri)	-	-	-	-	33.50 (3.66) ^b	34.50 (3.55) ^b	142.09 (46.36) ^c	36.93 (6.38) ^c
1.0–1.5 m								
<i>Agathis australis</i> (kauri)	-	-	-	-	-	-	-	-
<i>Dacrycarpus dacrydioide</i> (kahikatea)	-	-	-	-	1.39 (0.97) ^a	1.16 (0.81) ^a	0.57 (0.47) ^a	0.32 (0.25) ^a
<i>Dacrydium cupressinum</i> (rimu)	-	-	-	-	-	-	-	-
<i>Podocarpus totara</i> (totara)	-	-	-	-	-	-	9.93 (3.89) ^b	6.61 (2.16) ^a
<i>Prumnopitys ferruginea</i> (miro)	-	-	-	-	-	-	-	-
<i>Prumnopitys taxifolia</i> (matai)	-	-	-	-	-	-	-	-
<i>Alectryon excelsus</i>	-	-	-	-	0.41 (0.33) ^a	0.42 (0.36) ^a	-	-

(titoki)									
<i>Vitex lucens</i> (puriri)	-	-	-	-	5.49 (2.12) ^b	5.37 (2.15) ^b	82.69 (33.08) ^c	22.88 (8.05) ^b	
1.5–2.0 m									
<i>Agathis australis</i> (kauri)	-	-	-	-	-	-	-	-	-
<i>Dacrycarpus</i> <i>dacrydioide</i> (kahikatea)	-	-	-	-	-	-	-	-	-
<i>Dacrydium</i> <i>cupressinum</i> (rimu)	-	-	-	-	-	-	-	-	-
<i>Podocarpus totara</i> (totara)	-	-	-	-	-	-	-	-	-
<i>Prumnopitys</i> <i>ferruginea</i> (miro)	-	-	-	-	-	-	-	-	-
<i>Prumnopitus</i> <i>taxifolia</i> (matai)	-	-	-	-	-	-	-	-	-
<i>Alectryon excelsus</i> (titoki)	-	-	-	-	-	-	-	-	-
<i>Vitex lucens</i> (puriri)	-	-	-	-	-	-	10.27 (8.07)	2.51 (2.09)	

Note. In year-1 there were no roots >1 mm diameter to measure. Values in brackets represent the standard error of the mean. Values with different letters, within each parameter within each year were significantly different (Student-Newman-Keuls $P = 0.05$).