

Declining soil fertility does not increase leaf lifespan within species: evidence from the Franz Josef chronosequence, New Zealand

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Abstract: Leaf lifespan varies widely among plant species, from a few weeks to >40 years. This variation is associated with differences in plant form and function, and the distribution of species along resource gradients. Longer leaf lifespans increase the residence time of nutrients and are one mechanism by which plants conserve nutrients; consequently, leaf lifespan should increase within species with declining soil nutrient availability. The Franz Josef chronosequence is a series of post-glacial surfaces along which soil fertility declines strongly with increasing soil age. We used this fertility gradient to test whether leaf lifespans of six common indigenous woody species increased as soil nutrient availability declined. Leaf lifespan varied from 12.4 months in *Coprosma foetidissima* (Rubiaceae) to 47.1 months in *Pseudopanax crassifolius* (Araliaceae). These leaf lifespans sample 12% of the full range of leaf lifespans reported globally and occupy a relatively conservative portion of global leaf trait space. Contrary to our expectations, leaf lifespan of two species (*Pseudopanax crassifolius* and *Prumnopitys ferruginea*) decreased by 44–61% with increasing soil age and there were no other relationships between soil age and leaf lifespan. Across all species, leaf nutrient residence times increased by 85% for N and 90% for P with declining soil fertility, but this was caused by increased nutrient resorption efficiency rather than by increased leaf longevity. These data demonstrate that plants increase leaf nutrient resorption efficiency rather than leaf lifespan as a within-species response to long-term declines in soil fertility.

Keywords: foliar nutrients; indigenous tree species; intraspecific variation; leaf longevity; leaf trait; mean residence time; nitrogen; phosphorus; plant–soil interactions

Introduction

A long leaf lifespan is considered advantageous in nutrient-poor environments because leaf lifespan determines the residence time of resources retained in leaves, such as nitrogen (N) and phosphorus (P) (e.g. Monk 1966; Chabot & Hicks 1980; Eckstein et al. 1999; Aerts & Chapin 2000). The mean residence time (MRT) of nutrients in leaves is a critical aspect of whole-plant function; it determines individual plant performance by controlling rates of leaf photosynthesis and respiration, and also underpins the impact of a plant on ecosystem processes through litter quality and rates of litter decomposition. Leaf lifespan should increase as soil nutrient availability declines, and support for this hypothesis comes from both among- and within-species responses to soil nutrient availability. Comparisons among species have commonly demonstrated that plant communities on infertile soils typically support more evergreen species, or species with longer leaf lifespans, than communities on fertile soils (e.g. Monk 1966; Escudero et al. 1992). Further evidence has been derived from consistent relationships among species between leaf lifespan and leaf nutrient concentrations (e.g. Reich et al. 1997) that can be used to argue that declining leaf nutrient concentrations along soil fertility gradients should be accompanied by increasing investment in leaf structural carbohydrates and leaf lifespan. These predictions are based on the idea that the construction costs of leaves is higher in low-fertility environments and thus plants should protect their investment in leaves as nutrient availability declines (e.g. Lambers & Poorter 1992; Aerts & Chapin 2000; Grime 2001).

Evidence for within-species responses of leaf lifespan to soil fertility comes from natural fertility gradients, fertilisation experiments, and combinations of the two. Cordell et al. (2001) fertilised two sites with contrasting soil fertility along the Hawaiian soil chronosequence, and measured the response of leaf lifespan in the dominant tree species *Metrosideros polymorpha*. Fertiliser addition decreased leaf lifespan at the younger, fertile site as predicted, but leaf lifespan was unresponsive to fertiliser addition at the older, more infertile site. Furthermore, leaf lifespan of unfertilised trees was longest at the younger, fertile site counter to predictions that leaf

lifespan should be shortest on the most fertile sites. In this paper, we examine within-species variation in leaf lifespan along a long-term soil chronosequence that represents a strong fertility gradient at Franz Josef, New Zealand, to test whether leaf lifespan increases within species in response to declining soil fertility. The Franz Josef chronosequence is an outstanding natural fertility gradient; many common New Zealand woody species are widespread across this gradient, providing the opportunity to examine how key plant traits respond within species to changes in fertility (e.g. Whitehead et al. 2005). We determine how leaf lifespan varies within six common woody species along this gradient, combine those data with previously published estimates of nutrient resorption (Richardson et al. 2004, 2005) to estimate mean residence time (MRT) of N and P, and conclude by positioning our leaf lifespan data in global leaf trait space (GLOPNET; Wright et al. 2004) and discussing the range of leaf lifespans sampled by our six study species.

Materials and methods

The Franz Josef soil chronosequence is a series of postglacial surfaces in southern New Zealand (43° S, 170° E) that range widely in fertility (Stevens 1968). Richardson et al. (2004) described soil chemistry on nine surfaces (sites) and in this study data were gathered from eight sites that support tall forest, ranging in age from 60 to c. 120 000 years. Available soil P (ratio of organic P to total C) declines along the chronosequence from 5 mg kg⁻¹ (60 years) to 1 mg kg⁻¹ (120 000 years); Spearman rank correlation between available soil P and soil age $r = -0.92$, $P < 0.005$. Available soil N (aerobic mineralisable N) declines from 110 mg kg⁻¹ (60 years) to 15 mg kg⁻¹ (120 000 years); Spearman rank correlation between available soil N and soil age $r = -0.89$, $P < 0.005$. Mean annual temperature (1971–2000) is 10.0°C (Hessell 1982) and mean annual precipitation varies from 6.5 m (at sites 60–12 000 years old) to 3.6 m (sites 60 000–120 000 years old; site-specific precipitation given in Richardson et al. 2004).

Leaf lifespan was estimated in March 2002 from between two and six individuals per species per site (Table 1). These six species

Table 1. Mean leaf lifespan (± 1 SE) and age of the oldest living leaves for six New Zealand tree species along the Franz Josef soil chronosequence. Species are presented in order of increasing mean leaf lifespan. Differences among species were assessed using a GLM and model contrasts; means that share a letter are not significantly different at $P < 0.05$ (Crawley 2005). Leaf lifespan was \log_{10} -transformed to meet the assumptions of a parametric analysis. Plant names follow Allan (1961).

Species	Family	No. of sites sampled	Mean leaf lifespan (months)	Oldest living leaf lifespan (months)
<i>Coprosma foetidissima</i>	Rubiaceae	6	12.4 \pm 1.0 a	30
<i>Griselinia littoralis</i>	Cornaceae	7	14.8 \pm 1.1 a	30
<i>Metrosideros umbellata</i>	Myrtaceae	7	36.8 \pm 2.8 b	102
<i>Prumnopitys ferruginea</i>	Podocarpaceae	5	37.8 \pm 3.3 b	126
<i>Weinmannia racemosa</i>	Cunoniaceae	7	40.1 \pm 2.9 b	126
<i>Pseudopanax crassifolius</i>	Araliaceae	6	47.1 \pm 4.4 b	138

are all common along the sequence and account for 15–72% of total cover at each site, with the exception of the 60-year-old site where only one species (*Griselinia littoralis*) was sampled. Each species was sampled where it occurred along the chronosequence. Whole branches were sampled using orchard cutters or a shotgun and leaf lifespan was estimated by retrospective analyses of leaf scars (Lusk 2001; Cornelissen et al. 2003). Each branch was divided into annual segments within which we counted the number of living leaves and the number of leaf abscission scars. As leaves were sampled in autumn, we assumed that the youngest (current) segment was already 6 months old and that subsequent segments were progressively 12 months older than this. We used logistic regression with binomial errors (Crawley 2005) to model the relationship between segment age and leaf survival and to estimate the segment age when 50% of leaves had been lost, taken here as an estimate of median leaf lifespan. Leaf mass per unit area (LMA, g m^{-2}) and leaf nitrogen concentrations (N) were also measured on current-year foliage from each branch sample (Richardson et al. 2004, 2005). Leaf area was measured using a LiCor Area Meter, Model Li-3100 (Lincoln, NA, USA), leaf mass was measured on material oven-dried at 60°C for 48 h, and leaf nitrogen was determined from dried material using the acid digest and colorimetric methods described in Blakemore et al. (1987). Mean residence times for N and P were calculated using the formula in Kazakou et al. (2007) and our estimates of leaf lifespan from this study in combination with previously published estimates of nutrient resorption efficiency in these species at these sites (Richardson et al. 2005).

A general linear model (GLM) with model contrasts was used to test for differences in leaf lifespan among species and for the effect of site age on leaf lifespan within a species. Similarly, a GLM was used to test for an effect of site age on MRT of N and P. Site age, log-transformed, was used in these models to integrate across several measures of soil fertility that decline along the sequence (i.e. total P, mineral P, aerobic mineralisable N, ratio of organic P to total C). Replicates were individuals within species within sites.

We compared leaf lifespan, N and LMA at Franz Josef with a global dataset of leaf traits (GLOPNET; Wright et al. 2004). Our first goal was to determine how much of the global ‘trait space’ was sampled by the six species sampled at Franz Josef. To achieve this we used the functional richness index of Mason et al. (2005) to express the proportion of trait space sampled at Franz Josef as a proportion of the total space sampled by GLOPNET. Our second goal was to describe which part of global trait space was occupied by species at Franz Josef. All analyses were conducted in R v.2.9.1 (R Development Core Team 2009).

Results

Mean leaf lifespan varied approximately four-fold among the six species (GLM $F_{5,168} = 47.4$, $P < 0.001$; Table 1). The oldest living leaves ranged from 30 months (3 years) in *Coprosma foetidissima* and *Griselinia littoralis* to >120 months (>10 years) in *Prumnopitys*

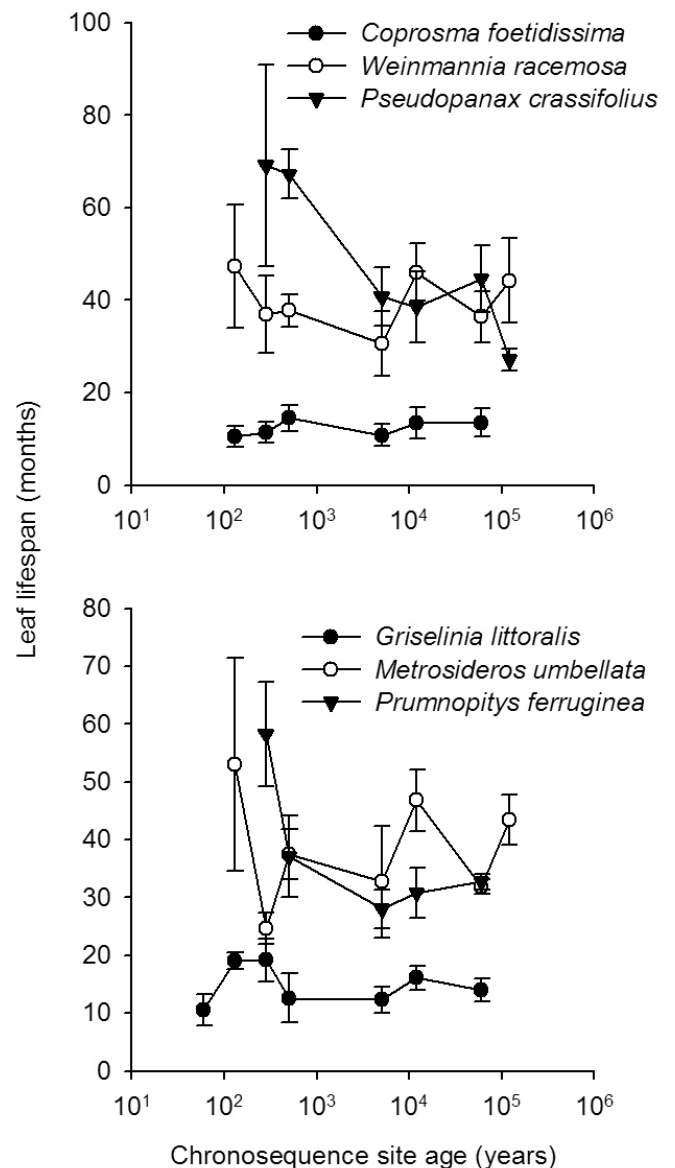


Figure 1. Response of leaf lifespan to soil age (i.e. an integrated measure of soil nutrient availability) in six dominant woody species along the Franz Josef soil chronosequence, New Zealand. Data are means ± 1 SE.

Table 2. Estimates of mean residence time (MRT, months) for nitrogen (N) and phosphorus (P) in leaves of six New Zealand tree species sampled where present as adults along the Franz Josef soil chronosequence. MRT was calculated from estimates of leaf lifespan (this study) and nutrient resorption efficiency (Richardson et al. 2005) using the formula in Kazakou et al. (2007). Data are means \pm 1 SE.

	Age of chronosequence site (years)								
	Mean	60	130	250	500	5000	12000	60000	120000
N MRT (months)									
<i>Coprosma foetidissima</i>	30 \pm 4		21 \pm 7	20 \pm 4	29 \pm 7	31 \pm 10	51 \pm 16	33 \pm 9	
<i>Griselinia littoralis</i>	28 \pm 3	14 \pm 5	47 \pm 6	26 \pm 5	22 \pm 7	19 \pm 4	25 \pm 4	48 \pm 11	
<i>Metrosideros umbellata</i>	105 \pm 8		87 \pm 17	78 \pm 13	114 \pm 16	107 \pm 36	96 \pm 15	110 \pm 11	131 \pm 8
<i>Prumnopitys ferruginea</i>	68 \pm 5			83 \pm 10	78 \pm 13	47 \pm 11	66 \pm 15	63 \pm 4	
<i>Pseudopanax crassifolius</i>	95 \pm 11			142 \pm 48	147 \pm 35	62 \pm 10	69 \pm 19	102 \pm 13	54 \pm 5
<i>Weinmannia racemosa</i>	95 \pm 8		101 \pm 30	66 \pm 16	77 \pm 9	61 \pm 13	145 \pm 19	114 \pm 18	114 \pm 19
P MRT (months)									
<i>Coprosma foetidissima</i>	26 \pm 4		15 \pm 5	12 \pm 2	28 \pm 5	33 \pm 13	38 \pm 10	29 \pm 8	
<i>Griselinia littoralis</i>	32 \pm 4	15 \pm 4	65 \pm 15	26 \pm 5	21 \pm 5	20 \pm 5	32 \pm 7	52 \pm 13	
<i>Metrosideros umbellata</i>	170 \pm 22		84 \pm 26	107 \pm 24	169 \pm 47	249 \pm 112	193 \pm 68	169 \pm 5	200 \pm 25
<i>Prumnopitys ferruginea</i>	98 \pm 10			88 \pm 26	116 \pm 28	66 \pm 24	104 \pm 19	114 \pm 13	
<i>Pseudopanax crassifolius</i>	139 \pm 26			276 \pm 175	201 \pm 28	79 \pm 14	67 \pm 16	158 \pm 22	80 \pm 18
<i>Weinmannia racemosa</i>	116 \pm 16		71 \pm 21	46 \pm 10	72 \pm 9	69 \pm 17	219 \pm 50	206 \pm 54	156 \pm 27

ferruginea, *Weinmannia racemosa*, and *Pseudopanax crassifolius*. Leaf lifespan within a species typically varied between 40% and 50% across all samples taken (Fig. 1). Mean leaf lifespan was only significantly related to chronosequence site age in two species; leaf lifespan decreased with site age in *Pseudopanax crassifolius* (GLM $F_{1,27} = 15.7, P = 0.0005$; Fig. 1) and *Prumnopitys ferruginea* (GLM $F_{1,22} = 5.0, P = 0.036$). Mean residence time (MRT) of N and P varied greatly among species and among sites and was commonly greater for P than for N (Table 2). The MRT of N increased significantly with chronosequence site age in *Metrosideros umbellata* (GLM

$F_{1,26} = 4.45, P = 0.045$) and *Pseudopanax crassifolius* (GLM $F_{1,27} = 6.38, P = 0.018$) and the MRT of P increased significantly in *Coprosma foetidissima* (GLM $F_{1,23} = 4.70, P = 0.04$), *M. umbellata* (GLM $F_{1,26} = 7.81, P = 0.01$), and *Weinmannia racemosa* (GLM $F_{1,28} = 18.2, P < 0.001$).

The six species sampled at Franz Josef sampled 12% of the full range of global leaf lifespans (Fig. 2) and occupied that part of the leaf economics spectrum characterised by conservative leaf traits; relatively long-lived leaves with low leaf nitrogen concentrations (Fig. 2). Indeed, the longest mean leaf lifespan estimated from an

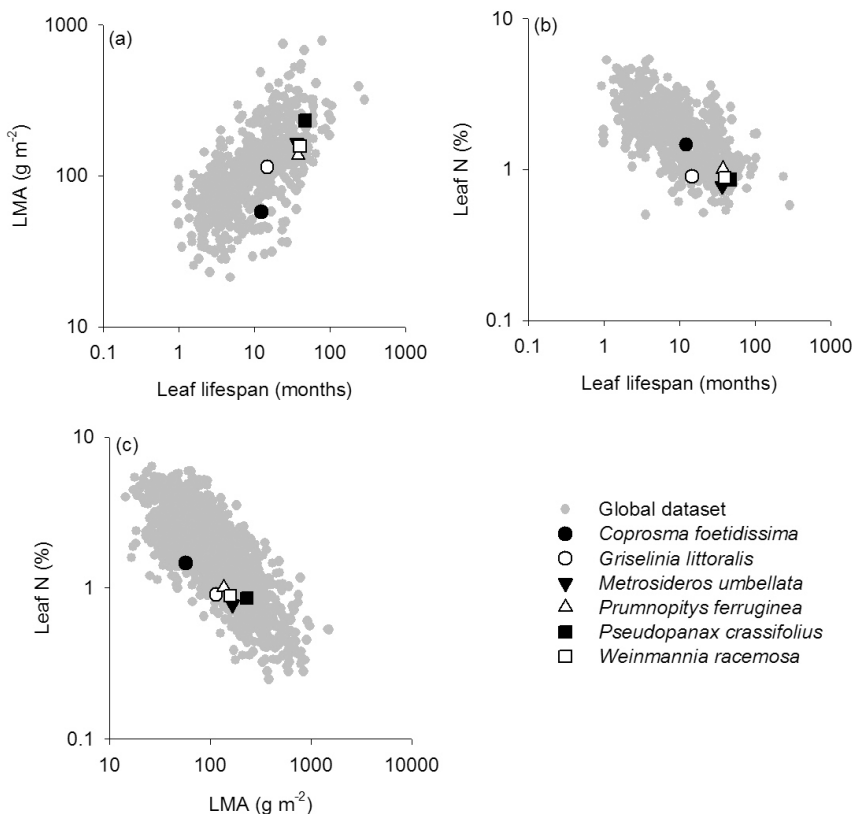


Figure 2. Bivariate relationships between leaf traits from a global dataset (GLOPNET; Wright et al. 2004) and from six species sampled along the Franz Josef soil chronosequence, New Zealand.

individual at Franz Josef (133 months, *Pseudopanax crassifolius* at the 250-year-old site) was towards the upper limit of leaf lifespans sampled globally (Fig. 2).

Discussion

We found no evidence that leaf lifespan increased within species as soil fertility declined. Leaf lifespan of *Pseudopanax crassifolius* decreased significantly with declining fertility but this response may be accounted for, in part, by heteroblastic shifts within the species. Individuals of *P. crassifolius* at the early chronosequence sites are younger individuals supporting longer, narrower, tougher pre-adult leaves ('transitional' sensu Gould 1993) that may have longer leaf lifespans than fully mature, adult leaves at the older sites (Dansereau 1964; Gould 1993). However, leaf lifespan of homoblastic *Prumnopitys ferruginea* also decreased significantly with declining soil fertility, counter to our predictions, suggesting that heteroblasty alone could not explain our results. Longer leaf lifespans on young, fertile sites have been reported from the Hawaiian chronosequence for *Metrosideros polymorpha* (Cordell et al. 2001) and the tree fern *Cibotium glaucum* (Walker & Aplet 1994). Cordell et al. (2001) suggested that other factors operating along the soil chronosequence, such as loss of soil structure and impeded drainage, may confound within-species responses of leaf lifespan to soil fertility, but these additional factors are poorly understood.

Previous studies at the Franz Josef chronosequence have demonstrated that both leaf and litter nutrient concentrations were highly plastic and exhibited strong directional responses to declining soil fertility (Richardson et al. 2004, 2005). When combined with the leaf lifespan estimates reported here, there was evidence that the MRT of both N and P increased in some species along the chronosequence (Table 2). These increases were largely driven by within-species shifts in resorption efficiency (Richardson et al. 2005). This result is unusual as the importance of leaf lifespan in determining intraspecific variation in MRT is thought to be equal to that of resorption (Eckstein et al. 1999) or substantially greater (Kazakou et al. 2007).

One explanation for the relatively invariant leaf lifespans reported here is that all the sites sampled are broadly 'nutrient-poor' (soil total P < 900 mg kg⁻¹; Richardson et al. 2004) and that intraspecific responses by leaf lifespan to soil nutrients only occur between extremely fertile sites and these more widespread, 'nutrient poor' sites. McGlone et al. (2004) proposed that low soil fertility throughout New Zealand accounted for the low incidence of deciduousness and short leaf lifespans in the woody flora. We suggest that limited plasticity of leaf lifespan within species is an additional dimension to that putative constraint on leaf lifespan. A similar suggestion was made by Cordell et al. (2001) to account for the absence of a response by leaf lifespan to fertiliser addition at old, nutrient-poor sites in Hawai'i. The extent of trait plasticity on infertile soils could be explored at Franz Josef using fertilisation studies as part of a wider effort to determine how environment controls key plant functional traits, both within and among New Zealand species. Finally, the significance of these within-species responses to community-level shifts in leaf lifespan are unknown as data are not available for all species at all sites. Compositional turnover among sites and the site-level dominance of species with distinctively short (e.g. *Aristolelia serrata* and *Melicactus ramiflorus*) and long (e.g. *Lagarostrobos colensoi* and *Phyllocladus alpinus*) leaf lifespans at the youngest and oldest sites, respectively, may override the absence of within-species shifts reported here.

The New Zealand woody flora is overwhelmingly evergreen (McGlone et al. 2004). The six species sampled here are all common woody species found throughout New Zealand. If the leaf lifespans we estimated at this site are typical of values for other similar species, our data suggest a mean leaf lifespan for New Zealand trees of between 2 and 3 years. Few strictly comparable, quantitative estimates are available for other evergreen woody species in New Zealand, but descriptive estimates of leaf lifespan from *Nothofagus* spp. (c. 13 months for *N. fusca*, 1–2 years for *N. solandri* and *N. solandri* var.

cliffortioides, and 3–5 years for *N. menziesii*; Russell 1936; Bussell 1968; Wardle 1984) correspond well with the range sampled at Franz Josef. While average leaf lifespans of 1–5 years are typical of temperate evergreen rainforest species (Wardle 1991; Lusk et al. 2003), the lifespans of individual leaves can be substantially greater. For example, the oldest living *Pseudopanax crassifolius* leaves sampled in this study were >11 years old (Table 1), despite the mean leaf lifespan being 3–4 years. Extraordinary individual leaf lifespans may be widespread among slow-growing species; Wardle (1963) estimated that some living leaves of the long-lived subalpine conifer species *Halocarpus biformis* could be >50 years old (600 months). These long-lived individual leaves must still be productive in order to be retained, suggesting they are well situated for photosynthesis and sufficiently robust to have avoided damage. However, robust leaves of high structural carbohydrate content would have low leaf-level productivity and thus the presence of very old leaves can only be characteristic of long-lived species with slow growth rates and low carbon gain requirements from individual leaves.

Despite only sampling six species at Franz Josef, we captured 12% of the total variation in leaf lifespan reported globally. These data from Franz Josef highlight that despite large-scale constraints on leaf construction by climate, local-scale mechanisms generate and maintain high trait diversity in a single ecosystem. Leaves at Franz Josef appeared to have low N content relative to their lifespans or their LMA, when compared with a global dataset (Fig. 2). Wright et al. (2001) demonstrated that leaves from high rainfall (1220 mm) environments in southern Australia had low leaf N concentrations relative to their LMA when compared with leaves from low rainfall (387 mm) environments. This was interpreted as a water conservation mechanism; a high leaf N concentration enables plants in dry environments to rapidly achieve a high internal CO₂ concentration at a low stomatal conductance. This interpretation could be used to argue that species at Franz Josef, operating under exceptionally high rainfall (3000 – >7000 mm) and constantly perhumid conditions, can achieve high internal CO₂ concentrations at comparatively low leaf N concentrations.

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