Is *Pittosporum patulum* Hook. f. threatened by pest herbivory in eastern South Island, New Zealand?

Geoffrey Rogers[1] and Susan Walker[2]

[1]Science and Research Unit, Science, Technology and Information Services, Department of Conservation, P.O. Box 5244, Dunedin, New Zealand (E-mail: grogers@doc.govt.nz)

[2]Landcare Research, Private Bag 1930, Dunedin, New Zealand

Abstract: We examined the threat status of the low tree *Pittosporum patulum* throughout its range in eastern South Island, based on plot-based sampling of habitat, defoliation by mammalian herbivores, demographic and dieback characteristics. Using environmental modelling (Land Environments of New Zealand), we found no explanation for the 'gap' in its disjunct distribution from Nelson–Marlborough–north Canterbury to south Canterbury as a component of upper montane *Nothofagus* forest and non-*Nothofagus* subalpine scrub. Size-classes in some populations suggest pulses of recruitment that may be phenologically or disturbance engendered, whereas others have demographic evidence for more continuous recruitment. In forest, disturbance appears not as important as environmental stress in maintaining understorey light gaps that allow it to reach reproductive maturity. A range of introduced mammalian herbivores appear to defoliate *P. patulum*, although consistently high levels of defoliation on adult foliage above ungulate browse–height point to possums (*Trichosurus vulpecula*) as the main pest. Demographic data and herbarium records show adults are few in Nelson–Marlborough and north Canterbury, where the species' viability is in question despite many juveniles. Alternatively, south Canterbury populations, although browsed, show less dieback, especially in subalpine scrub. Its variable demography may be related to the history of possum colonisation throughout its range. Evidential support is provided for its threat ranking of 'nationally endangered'.

Keywords: Introduced pests; New Zealand; Pittosporaceae; rarity; threatened vascular plants.

Introduction

Dicotyledonous trees and shrubs account for a relatively high proportion of New Zealand's rare and threatened vascular plant flora (Rogers and Walker, 2002). Most of New Zealand's threatened trees are restricted to the northern North Island. However, *Pittosporum patulum* Hook. f. (Pittosporaceae) is an endemic low tree (maximum height = 6 m) of montane forest and subalpine scrub that has been recorded only in the South Island from west Nelson and Marlborough to north Otago mainly on the eastern side of the Main Divide.

Long-standing botanical and conservation interest in *P. patulum* is reflected in numerous herbarium records, along with many unvouchered records and accounts of recently established monitoring studies that appear on the files of land-administering Government departments. It has a restricted distribution within otherwise widely distributed *Nothofagus* forest and subalpine scrub, with an apparent absence in central Canterbury. It shows both heteroblastic (height

dimorphism involving changes in leaf and/or shoot features) and heterophyllic (changes in leaf features during shoot ontogeny) development, and in this it has some equivalence to the central North Island congeneric low tree, *P. turneri*.

Whereas the morphology of *P. patulum* is well documented, its biogeography, demography, habitat preferences, reproductive behaviour, and conservation status are poorly understood. In general, its subalpine scrub habitat is a scientifically neglected ecosystem, perhaps partly since it contains few rare or threatened species (Rogers and Walker, 2002). Nevertheless, there is accumulating evidence of unsustainable levels of defoliation of *P. patulum* by herbivores (Joyce, 1993; van Eyndhoven and Norton, 2001). Herbarium records from Nelson and Marlborough that extend from the late 19th century to 1999, along with anecdotal accounts, indicate the disappearance of previously abundant adult trees, particularly from northern populations, since the late 1970s (Eagle, 1982:269). Other than inference from herbarium material, there is no historical demographic data to use as a comparison

with modern data from which to judge trends. Comparatively recent discoveries of *P. patulum* in the upper Waitaki River catchments of south Canterbury, with numerous, apparently healthy, adult trees, contrast with the Nelson–Marlborough situation (van Eyndhoven and Norton, 2001). On the basis of defoliation or stem decapitation, introduced herbivores have been implicated in the apparent decline of *P. patulum*, particularly in Nelson and Marlborough. Hares (*Lepus europaeus occidentalis*), red deer (*Cervus elephus scoticus*), goats (*Capra hircus*), and, in particular, brushtail possums (*Trichosurus vulpecula*) are suggested pest herbivores (Joyce, 1993; van Eyndhoven and Norton, 2001).

In response to these concerns, we assess the status and condition of *P. patulum* stands across most of its range. Specifically, we examine variations in population structure, habitat physiography, plant community composition, phenology, and correlates of defoliation

and dieback that may point to predisposing factors for its apparent decline. Adverse browsing and grazing by introduced herbivores affects 62% of New Zealand's threatened flora (Dopson *et al.*, 1999). *Pittosporum patulum* is a potentially iconic tree for this threat syndrome in montane *Nothofagus* forest and subalpine scrub of eastern South Island.
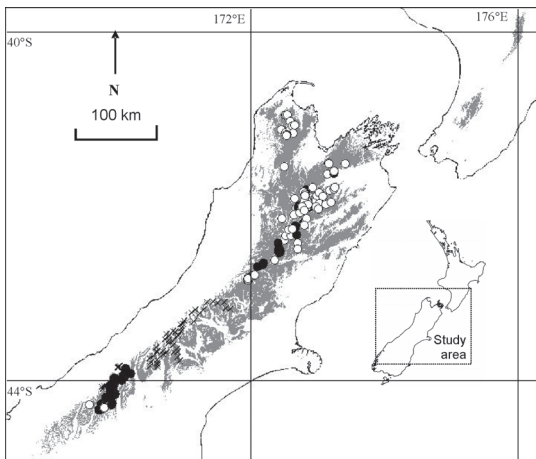
Methods

Data collection

Information on the distribution of *P. patulum* was obtained from WELT and CHR herbarium records, the National Vegetation Survey databank (NVS), anecdotal information from other botanists, and information contained in file notes of the Department of Conservation. The latter included documentation from one of its predecessor organisations, the New Zealand

Table 1. Location of sample sites of *Pittosporum patulum* from the present study, along with other (*) unsampled, representative records from CHR, WELT, Department of Conservation file notes, and National Vegetation Survey (NVS) databank (Landcare Research, Lincoln) used to compile Fig. 1. Number of multiple populations sampled in each catchment given in brackets. **indicates not mapped in Fig. 1 because of lack of reliable grid reference.

Catchment or range	Location
Nelson	
Cobb River	Lake Sylvester*, Cobb Reservoir (2), mid Cobb Valley (2), Cobb Ridge (between Lockett and Peel ranges)*, Patulum Pond, Myttons Creek, Hannah Creek, near outlet of Cobb Valley*, ridge between Takaka and Cobb rivers*
Mt Peel*	
Waingaro River	Devil River Peak*, Fuller Stream*, Lindsay Creek*, Lockett Range*
Snowden Range*	
Boulder Lake	Snow River*, Opposite Darby Pond*, Portia Creek*
Owen Range	Blue Creek*
Marlborough-north Canterbury	
Richmond Range	Pine Valley below Mt Fishtail*, Mt Patriarch, Lake Chalice*, Goulter River*, Goulter River above Lake Chalice**
Bryant Range	Mt Starveall*, Starveall Hut*
Big Bush Forest	Duckpond Stream*
Wairau River	Southern Red Hills*, main Wairau Valley (2), St Ronans Stream*, St Ronans Well*, Begley Creek*, Connors Creek*, Turkeys Nest in Wye River*, Wye River*, Hamilton River*, No Mans Creek*, Six Mile Creek (2)*, Sandfly Stream (2)*, Judges Creek**, Rough Creek*, north of Lee Creek*, Lee Creek (2), Rag and Famish Stream
Waihopai River	Right Branch*
Leatham River	Upper Station Creek*, upper Leatham River*, Flat Stream*, near Weka Stream*, Gordons Creek*
Branch River	Silverstream (2)*, Misery Stream (2)*, Top Branch Hut*, Lost Stream (3)*
Sabine River	East Branch*
Travers River	Travers River headwaters (2), above Hopeless Creek confluence, Cupola Basin*
St Arnaud Range	Parachute Rock Track at Lake Rotoiti*, Motupiko River in Tophouse Scenic Reserve, near Borlase Stream at Lake Rotoiti*, Connors Creek**
Howard Valley	Cedric Stream*
Acheron River	Oldham Stream a tributary of Alma River*
Spenser Mountains	Lake Guyon in St James Station*, Henry River in St James Station*, Ada River in St James Station*, McKellar Stream in Matakitaki Valley*, Mt St Patrick in Williams Valley*, Glacier Gully*
Hope River	Kiwi Stream, unnamed tributary
Cox River	mid Cox River*, Ellis Stream (2), unnamed tributary
Hurunui River	South Branch (2), Three Mile Stream at Lake Sumner
Waiau River	Maling Pass*, The Poplars at Poplar Stream*

Table 1 contd.

Boyle River	Maritana Stream (2), mid Boyle River (3), Boyle Hut Stream, Rokeby Stream
Clarence River	Lake Tennyson, Duncans Stream, Edwards Flat in Horrible Stream, Amuri Skifield Road**

South Canterbury

Tasman River	Bush Stream
Dobson River	Kennedy Hut, Kennedy Monument, Reardon Biv (2), Waterfall Hut, Watson Stream
Hopkins River	Opposite Elco Stream, Huxley River North Branch (2), Huxley River South Branch, Huxley River (2), North Branch Temple Stream (2), South Branch Temple Stream (2), North Elco Stream, South Elco Stream, Elco Stream, Maitland Stream (2)
Ahuriri River	Canyon Creek, Hodgkinson Creek*, mid Ahuriri River

North Otago

Dingle River	Top Dingle Hut (2), west tributary in upper Dingle River
Hunter River	Cascade Creek*

Figure 1. Present sample sites (○) supplemented with several historical records (●) of *Pittosporum patulum* in New Zealand listed in Table 1, and its potential environmental envelope (shaded) in terms of climate and soils data from Land Environments of New Zealand (Leathwick *et al*., 2003). Sites searched without finding *P. patulum* are shown as crosses (×).
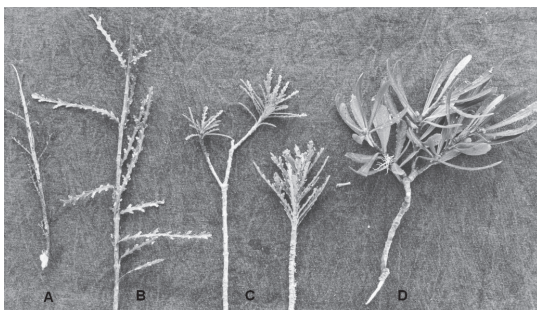
Figure 2. Ontogeny of *Pittosporum patulum* according to four leaf stages: A, seedling; B, sapling; C, subadult; D, adult.

Forest Service. A site record database was assembled from these records (Table 1; Fig. 1). A subset of these records was subjectively selected for plot sampling with the intention of covering, broadly, its geographic range. However, we view our coverage of the species' Nelson range as limited and probably unrepresentative and, accordingly, suggest that interpretation of those results be treated with caution. Further, we reconnoitred major valleys within the species' mid–Canterbury disjunct gap and the upper reaches of two southern valleys, undertaking a thorough survey at numerous sample sites within each that had forest or subalpine scrub vegetation not dissimilar to its communities north and south of the gap (Fig. 1). This unsuccessful reconnoitre and survey covered the Rangitata, Clyde, Havelock, Lawrence, Cass, Godley, Macauley, Rakaia, Wilberforce, Avoca, Harper, and Broken River catchments within the gap (Fig. 1). In addition, we surveyed unsuccessfully in the upper Landsborough and Hunter rivers in south Canterbury and South Westland (Fig. 1).

P. patulum has a patchy distribution of discrete populations or stands in forest and in subalpine scrub. For sampled stands, its population structure was estimated in variable area, rectangular plots selected and positioned to contain greater than five individuals and to extend to the limits of each discrete patch. Accordingly, plot size varied with the density of *P. patulum*, ranging from 4 m² to 10 000 m². For each *P. patulum* plant, we recorded stem diameter (above the basal swelling), stem height, life stage of leaves, amount of leaf defoliation excluding that attributable to insects (in four classes: 0, 1–33%, 34–67%, and > 67%), amount of dieback (in four classes: 0, 1–33%, 34–67%, and >67%), and reproductive features, including presence of flowers (male or female) and fruit capsules (fresh or dried and dehisced). We categorised plant ontogeny according to four leaf types (Fig. 2): seedling, sapling, subadult, and adult

(foliar stages 1–4). Dieback was assessed as the percentage of dead branches or branchlets (but not recently defoliated live twigs) over the whole of the canopy and not those below the leaf-bearing parts of the stem that result from stem extension (Payton *et al.*, 1999). Where dead stems with sound wood were encountered, wood discs were cut at intervals up the stem and sanded and aged to assess radial increment and vertical extension growth rates. Demographic sampling was not used for density estimates or relationships with forest community population structures.

Site and vegetation community characteristics were described for each plot in uniform vegetation and topography, following the 'reconnaissance' technique of Allen (1992). Environmental variables collected at each site included elevation, aspect, slope, and drainage (scored from 1 = poor to 5 = good). Aspect was converted to two bearings, representing degrees north (i.e. 0° = due south, 180° = due north) and degrees east (i.e. 0° = due west, 180° = due east). At each of the *P. patulum* plots and for each of the surveyed sample sites where it was not found within its disjunct gap, underlying data surfaces from LENZ (Land Environments of New Zealand; Leathwick *et al.*, 2003) were used to obtain estimates of climate (mean annual temperature, minimum temperature of the coldest month, mean annual solar radiation, June solar radiation, October vapour pressure deficit, the ratio of rainfall to potential evapotranspiration, annual water deficit) and estimates of substrate characteristics (soil drainage, soil age, phosphate, calcium, induration and particle size).

All plots, including those within the disjunct gap reconnoitre, were sampled between 1998 and 2001, in the spring to autumn period. NZMS 260 grid references of sampling plot, historic records additional to the plots (multiple records from catchments were reduced to a representative few that extended between the upper and lower distributional limits within each catchment), and sites searched unsuccessfully for the species were used to compile a distribution map (Fig. 1).

Data analysis

Multivariate analyses were used to examine the occurrence of *P. patulum* in community types and along environmental gradients within the 156-plot dataset. A cluster analysis classification (Clifford and Stephenson, 1975; flexible sorting system, Jaccard measure of dissimilarity in species presence, ß = 0.25) was used to derive eight groups of plots (hereafter 'plant communities'). Geographical distribution, environment and flora, and the demography and health of *P. patulum* were compared between these communities using Tukey's tests.

A Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) ordination was used to arrange the plots along gradients of vegetation composition. Simple regressions were used to identify relationships of environment factors, and the demography and health of *P. patulum,* with the two principal gradients (ordination axes). Vectors of significant correlations were plotted on the ordination axes, together with the average scores of plots within each plant community and within each catchment.

To determine whether the environment differs between the zone where *P. patulum* has been recorded and the mid-Canterbury zone where it has never been recorded (including the catchments searched without success in the present study: i.e. the disjunct 'gap'), we calculated the environmental envelope of *P. patulum* based on its current and historical range. We identified the upper and lower limits of each of the climate and substrate variables underlying the LENZ classification (Leathwick *et al.*, 2003) across all present and historical *P. patulum* plots. We then mapped all of the Level IV land environments in LENZ that fell within this environmental envelope, using GIS ArcView (Environmental Systems Research Institute, 2000). We overlaid locations of current and historical records of *P. patulum*, and sites searched unsuccessfully within its disjunct gap and to the south, on the mapped environmental envelope.

For demographic and foliar condition analyses, we divided plots into two higher-order community types: forest plots are those classified in one of the five forest communities (A to E) and scrub plots are those classified within one of the three scrub communities (F, G and H). The dataset was further divided into two provenance subsets, i.e. northern (including only west Nelson, Marlborough, north Canterbury plots) and southern (south Canterbury and north Otago plots).

We estimated and compared (using Duncan's test for differences in slopes of regression lines; Snedecor and Cochran, 1980) allometric relationships between height and diameter for plants in each of the four foliar stages between forest and scrub associations in the northern and southern provenances. We used chi-squared tests to formally compare proportions of plants in the four foliar stages between northern and southern provenances and between forest and scrub.

We estimated and compared (again using Duncan's test for differences in slopes of regression lines; Snedecor and Cochran, 1980) radial increment growth rates and life spans of *P. patulum* from collected dead stems of 26 forest and 18 scrub plants. We then used the age v. stem diameter and height v. diameter allometric relationships, to estimate the ages of populations of *P. patulum* plants in the northern and southern provenances at each of the four foliar stages. We also used the age v. stem diameter and the allometric

relationships to estimate the age of plants at their sampled heights in forest and scrub, and in northern and southern populations. Nine of the 26 dead stems from forest and six of the 18 dead stems from scrub were of sufficient durability to cut discs from their base and tops. We compared the mean vertical growth rates from these forest and scrub samples. Because the dead wood of *P. patulum* appears to have low durability and the sample of age estimates from discs is accordingly small, the question of representativeness of the stem age and growth rate estimates implies caution in their application.

We used chi-squared tests and simple regression to determine whether defoliation and dieback were related to demography (represented by foliar stages, stem height and stem diameter) in the whole dataset and separately for different community types (forest and scrub), provenances, catchment groups and individual catchments.

Results

Distribution

Pittosporum patulum is widely distributed in the northern and central South Island (Fig. 1, Table 1), but is not known from west of the Central Sedimentary Belt of west Nelson (Lillie, 1980) or west of the Main Divide further south. It has a patchy distribution in west Nelson, is widespread in Marlborough and north Canterbury, and has a narrow range in southwest Canterbury (Fig. 1). Our failure to find it within mid Canterbury corroborates the impression from herbarium vouchers and other records that the species has a disjunct distribution, being absent from western mid-Canterbury, specifically the catchments of the Pareora, Opihi, Orari, Rangitata, Ashburton, Rakaia, and Harper–Avoca rivers. It has not been found south of the Dingle Burn and Hunter rivers in north Otago.

Environmental range

The predicted environmental range of *P. patulum* using climate and soil variables from the LENZ database extends beyond the zone of present and historical records to include: an extension south beyond the southern limit in north Otago to cover much of Mt Aspiring National Park in west Otago; the mid-Canterbury disjunct 'gap'; eastward into the Inland and Seaward Kaikoura Ranges of Marlborough; and an extension north from west Nelson and Marlborough to the Tararua and Ruahine ranges of the North Island (Fig. 1).

Habitat

Pittosporum patulum tends to be concentrated in the mid to upper reaches of mountain catchments, particularly the tributaries of arterial valleys. *P. patulum* is found across a spectrum of mountain valley habitats and plant communities from 670 to 1260 m a.s.l., with a mean altitude of 895 m a.s.l.

In *Nothofagus* forest, it is concentrated in light gaps associated with the subalpine treeline; the inverted treeline of valley floors; slips generated by snow avalanche, debris flow, rock fall or slides; the margins of steeply-incised stream courses; about rock bluffs; and fire-created forest margins. It may occur in tree-fall-gap-sized canopy openings, in larger canopy gaps created by cyclonic windthrow, or even beneath a closed *Nothofagus* canopy, but seldom if ever as adults in small gaps or beneath closed canopies.

In non-*Nothofagus* subalpine scrub or low forest, *P. patulum* is not restricted to canopy openings or margins. It can 'hold its own' on all valley positions where canopy stature permits it to escape shaded understoreys. However, it has a curiously spasmodic pattern across zones of ostensibly suitable habitat. Species composition of subalpine scrub varies, but common dominants include *Phyllocladus alpinus*, *Dracophyllum longifolium*, *Polystichum vestitum*, *Aristotelia fruticosa*, small-leaved coprosmas, *Griselinia littoralis*, *Podocarpus nivalus*, *P. hallii*, *Brachyglottis cassinioides*, *Hoheria lyallii* and *Pseudopanax colensoi*. Sporadically, adult *P. patulum* trees are emergent above scrub canopies. It is only predictably absent from the tallest old-growth *P. alpinus*-dominated subalpine scrub-low forest.

The species has no particular aspect preference, although most sites are steep (average 29°; Table 2). Greywacke is the basement geology for the majority of eastern locations of *P. patulum* from Marlborough to north Otago. In west Nelson, it occurs on volcanic conglomerates, sandstones, and siltstones, pelitic schist, but not sedimentary argillite, sandstone, or schist. Its southern limit in the Dingle Burn and lower Hunter Valley, North Otago, coincides with a distinct change in geological substrate from greywacke to schist (New Zealand Geological Survey, 1972). However, its apparent absence from mid-Canterbury is not correlated with a geological discontinuity.

Reproductive biology

Few sampled populations had flowers or fruit. Where flowers and fruit occurred, plants almost invariably had adult foliage. However, flowers were recorded on one subadult plant in Dingle Stream, North Otago. The South Branch of Temple Stream provided the only flowering population sufficiently large to reliably estimate an adult sex ratio, with 14 (45%) males and 17 (55%) females.

A

B
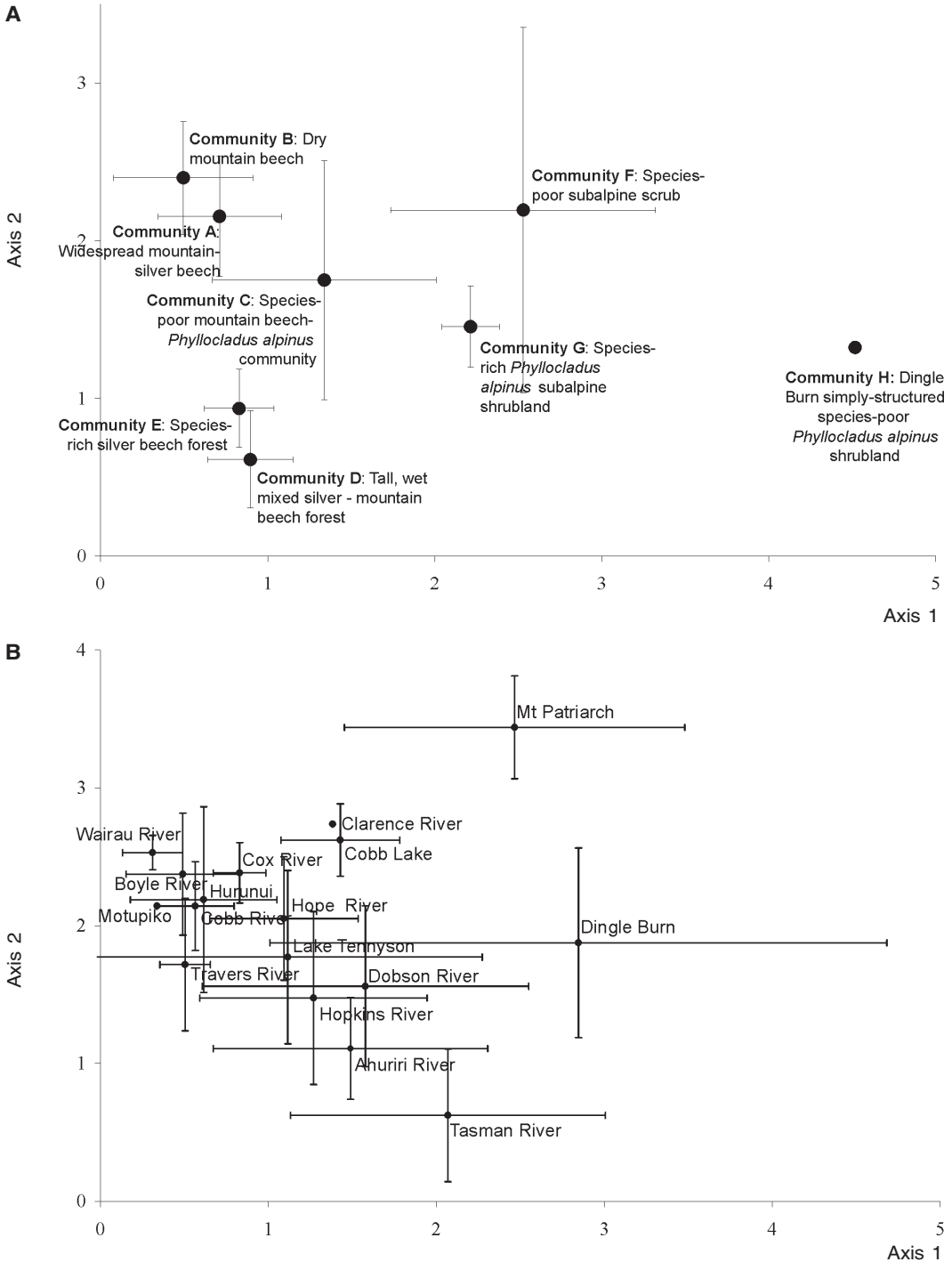
Figure 3. A, Community positions ±1 SD from the cluster analysis classification and B, site (catchment) positions ±1 SD on Axes 1 and 2 of a DCA ordination of species composition.

Table 2. Mean demographic, environmental, and geographic characteristics of eight communities containing *Pittosporum patulum*. Superscript letters in common indicate not significantly different by Tukey's test, where significant (or valid).

Community	Forest				Scrub			
	A	B	C	D	E	F	G	H
	Widespread mountain-silver beech forest	*Dry mountain beech forest*	*Species-poor mountain beech/ Phyllocladus alpinus forest*	*Tall, wet mixed silver-mountain beech forest*	*Species-rich silver beech forest*	*Species-poor subalpine scrub*	*Species-rich Phyllocladus alpinus subalpine scrub*	*Species-poor Phyllocladus alpinus scrub*
Pittosporum patulum								
Number (%) of recorded plants	594 (32)	126 (7)	375 (21)	64 (4)	171 (9)	174 (10)	312 (17)	12 (1)
Number of plots recorded	59 (38)	24 (15)	19 (12)	6 (4)	20 (13)	15 (10)	11 (7)	3 (2)
Average height (mm)	1558^b	2182^a	1645^b	2430^a	1364^b	2542^a	2274 ^{a}	2600 ^{a}
Average diameter (mm)	13^d	23^{bc}	17^{cd}	30^{ab}	13^{cd}	41^a	21^{bc}	28^{abc}
Average foliar stage (mean score)	1.9^c	2.2^b	2.1^b	2.8^a	1.7^c	2.9^a	2.7^a	3.0^a
Average defoliaton (mean score)	0.8^b	0.8^b	1.3^a	0.8 ^{b}	1.0^b	0.3^c	0.2^c	1.7^a
Average dieback (mean score)	0.9 ^{ab}	1.0^a	0.3^c	0.6^{bc}	0.7^b	0.4^c	0.8^a	0.0^c
Average environmental characteristics								
Elevation (m a.s.l.)	947^{ab}	933^{ab}	1017^a	841^b	927^{ab}	1041^a	950^{ab}	1040^a
North aspect (max 180º)	112^a	114^a	72^b	121^a	100^{ab}	105^{ab}	92^{ab}	110^{ab}
East aspect (max 180º)	76^{ab}	62^{ab}	55^b	95^{ab}	83^{ab}	100^{ab}	83^{ab}	160 ^{a}
Slope (º)	37	34	33	29	24	33	35	10
Drainage score (1–5)	1.9^a	1.9^a	2.0^a	2.0^a	1.6^b	2.0^a	2.0^a	2.0^a
Annual rainfall (mm)	2474^b	1748^c	2337^{bc}	3803^a	3177^{ab}	2639^b	3240^{ab}	1964^{bc}
Max. temperature warmest month (ºC)	19.2^{ab}	19.6^a	19.1^{ab}	19.8^a	19.4^a	18.5^b	19.3^{ab}	18.7^{ab}
Min. temperature coldest month (ºC)	-2.7	-2.9	-3.0	-2.5	-2.6	-2.6	-2.6	-3.0
Mean monthly temperature (º)	7.1	7.1	6.6	7.5	7.0	6.8	6.9	6.5
Lowest monthly rainfall: pet ratio	1.9^{bc}	1.4^c	1.9^{bc}	3.2^a	2.6^{ab}	2.1^{bc}	2.8^{ab}	1.5^{bc}
Min. monthly humidity (%)	69.2^a	66.0^c	66.4^{bc}	69.4^a	69.1^a	68.4^{ab}	67.6^{abc}	67.4^{abc}
Min. monthly vapour pressure deficit (%)	0.12^a	0.12^a	0.11^{ab}	0.12^{ab}	0.11^{ab}	0.11^{ab}	0.11^{ab}	0.09^b
Max. monthly solar radiation (MJ m^2 day^{-1})	23.2^a	23.3^a	23.0^{ab}	22.6^b	22.7^b	23.4^a	22.7^b	22.8^{ab}
Min. monthly solar radiation (MJ m^2 day^{-1})	5.4^a	5.3^{ab}	5.1^b	5.1^b	5.1^b	5.4^a	5.1^b	4.9^b
Community								
Species richness	26.7^b	15.3^c	9.8^c	10.5^c	27.1^{ab}	18.3^c	34.2^a	8.0^c
Maximum canopy height (mm)	11831^{ab}	10042^b	9982^{bc}	15000^a	14350^a	5167^d	6227^{cd}	3500^d
Provenance (catchment and no. of plots)								
[1]Northern	C5 P1 T8 W5 B12 H2 U4 X8	M1 W4 B12	L4		T2 U1	C2 P4	A1	
[2]Southern	D4 H10	D2 H5	T2 D1 H7 A2 I3	H6	D1 H12 A4	T2 D2 H4	D4 H6 A1	I3

[1]Northern Provenance: C = Cobb Catchment, P = Mt Patriarch, M = Motupiko, T = Travers River , W = Wairau River, L = Lake Tennyson, A = Clarence River, B = Boyle River, H = Hope River, U = Hurunui River, X = Cox River.
[2]Southern Provenance: T = Tasman River, D = Dobson River, H = Hopkins River, A = Ahuriri River, I = Dingle Burn.

Plant communities, vegetation gradients and environmental relationships

The classification defined eight plant communities containing *P. patulum*. Five are forest communities (A to E), and three are scrub (F to H; Fig. 3; Table 2).

Community A: *Widespread species-rich mountain beech (*Nothofagus solandri *var.* cliffortioides*) forest with silver beech (*N. menziesii*)*
A high percentage (38%) of recorded *P. patulum* grew beneath a canopy of tall to intermediate-height mountain beech and (in about a third of sites) silver beech. Most recorded sites in Community A were in the northern provenance and on north-facing slopes, with species-rich understories. Young *P. patulum* plants predominated, and as a result, average height and diameter were low. Their populations showed moderate defoliation and quite a lot of dieback.

Community B: *Dry mountain beech forest*
A smaller proportion of *P. patulum* plants were recorded in tall (~10 m) mountain beech forest in relatively warm, low-rainfall, low-humidity environments (Table 2). The community was moderately species-rich. Juvenile *P. patulum* plants predominated in recorded populations, although a relatively high percentage of plants (29%) were in the older foliar stages 3 and 4, and in the upper height and diameter categories; thus, the average diameter of plants was moderate and the average height was relatively tall. There was moderate defoliation and abundant dieback.

Community C: *Species-poor mountain beech/* Phyllocladus alpinus *forest*.
Distribution: A fifth (21%) of *P. patulum* plants were recorded in this variable community at high-elevation sites on southwest aspects. Foliar class 2 plants predominated in *P. patulum* populations (62%) and there were relatively few individuals in the adult foliar class (4) and in the tallest height class. We recorded a considerable amount of defoliation, but little dieback was evident.

Community D: *Species-poor, low-elevation, tall, wet mixed silver beech-mountain beech forest*
Very few (4%) *P. patulum* plants were recorded in this community, which is restricted to moderately low elevation sites in the Hopkins catchment in south Canterbury, where maximum temperatures, annual rainfall and the ratio of average rainfall to potential evapotranspiration (PET) are all relatively high. The canopy was tall, with silver beech constant and occasional mountain beech. Few juvenile *P. patulum* plants were recorded, and adult (foliar stage 4) plants accounted for nearly half of the populations. Larger height and diameter classes were well represented. Moderate defoliation and dieback were evident.

Community E: *Species-rich silver beech forest*
Small numbers of *P. patulum* plants (9% of total) occurred in this widespread, but predominantly southern, tall silver beech forest type, which occupied soils with relatively poor drainage. Half of the recorded sites contained mountain beech in the canopy, and red beech (*Nothofagus fusca*) was recorded in some of the Travers and Hurunui valley sites. There were smaller proportions of older and larger plants of *P. patulum* than in any other plant community (2% and 6% in foliar stages 3 and 4, respectively). Average plant height in populations was therefore also lowest, and stem diameters were small. Plants showed relatively high defoliation and moderate dieback.

Community F: *Species-poor subalpine scrub*
Ten percent of *P. patulum* plants were recorded in this high-elevation scrub type, which occurred in both northern and southern provenances. We recorded relatively few juvenile *P. patulum* plants (foliar stage 1) and a predominance of adults (34% were foliar stage 4). Average height and diameter of *P. patulum* were greater than in any other community (except the average height for one Dingle Burn plot in Community H, see below). Little defoliation or dieback were recorded.

Community G: Species-rich *Phyllocladus alpinus* subalpine scrub
Seventeen percent of *P. patulum* plants were recorded in this species-rich, short-canopied scrub community in south Canterbury. *Phyllocladus alpinus* was a constant species, and *Aristotelia fruticosa* and *Dracophyllum longifolium* were common. The high percentage (33%) of *P. patulum* plants in foliar stage 4 was similar to that in species-poor subalpine scrub. However, juveniles (foliar stage 1) were slightly better represented, and thus average plant height was less than in species-poor subalpine scrub and average stem diameter was much lower. Less defoliation was recorded than in other communities and we noted little dieback.

Community H: Dingle Burn simply structured, species-poor *Phyllocladus alpinus* scrub
Just 12 *P. patulum* in foliar stage 3 (<1% of the total) were recorded in this low-canopied community on three sites on east-facing slopes in the Dingle Burn. Defoliation was pronounced but we recorded no dieback.

The main vegetation gradient identified by the ordination (Fig. 3A) runs from tall forest communities (A to E: both silver beech and mountain beech) at the left (low scores), to subalpine scrub communities (F to H) with high scores at the right. Simple regressions show minor but significant decreases in the average elevation of sites along this axis from forest to scrub,
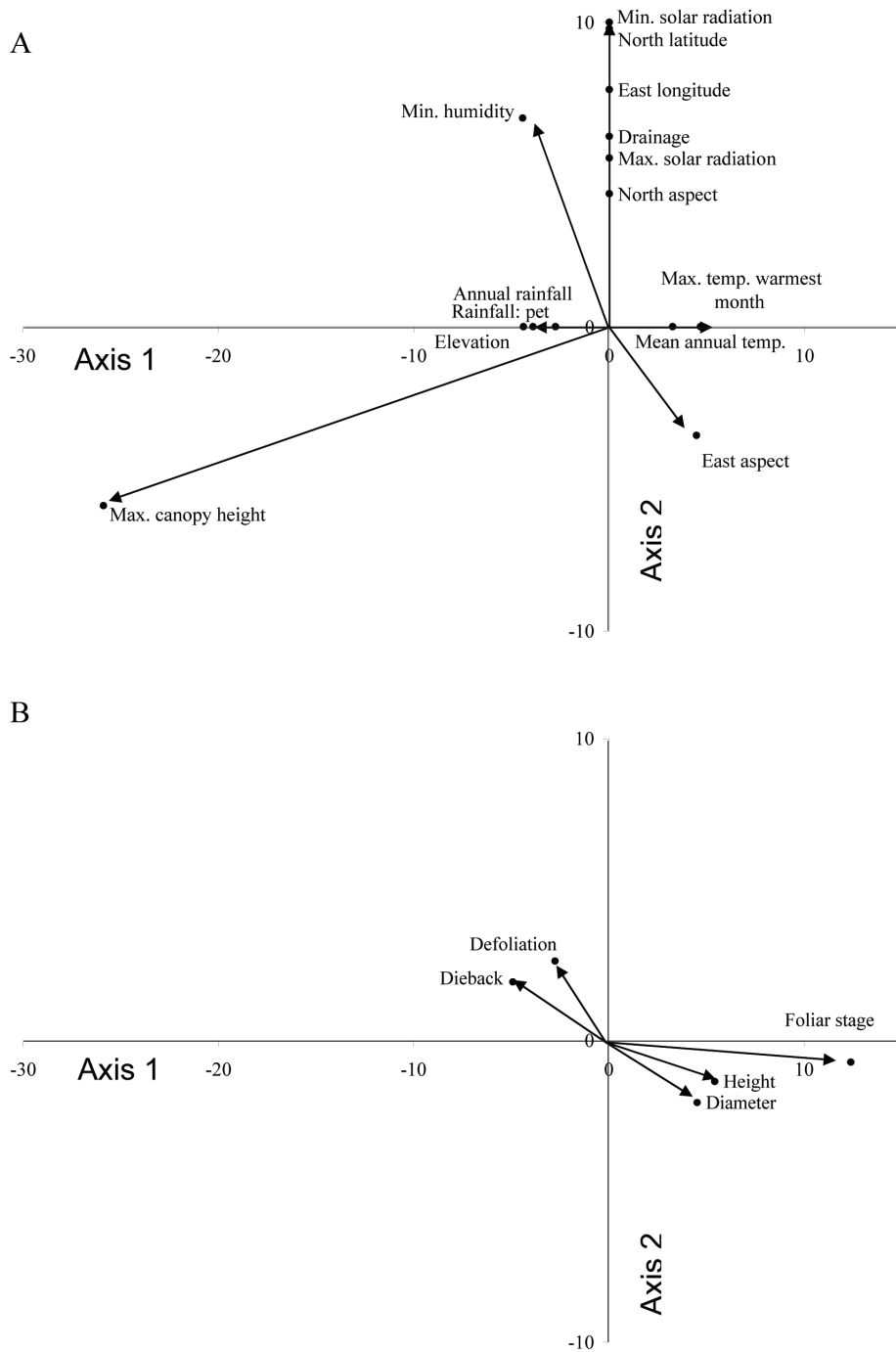
Figure 4. Direction and percentage of variation explained by simple regressions of A, environmental and B, demographic variables on Axes 1 and 2 site scores, derived from the DCA ordination of species composition. Axis units are percent variation explained.
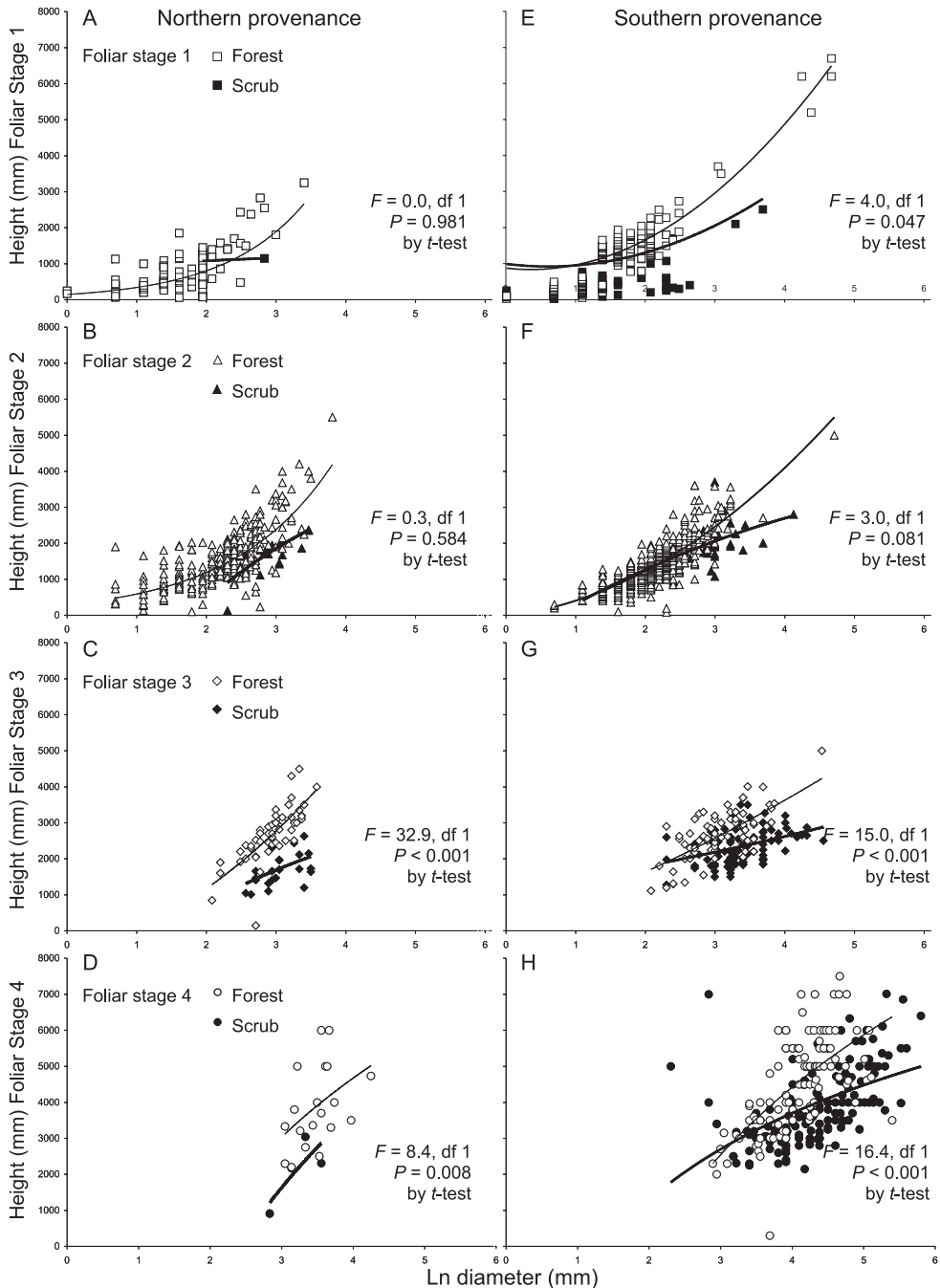
Figure 5. Relationships between plant height and stem diameter for *Pittosporum patulum* in four foliar stages as sampled in forest and scrub communities and in northern and southern provenances (for explanation of foliar stages and provenances, see Methods). We show best fit regression relationships and *P*-value where probability of fit is significant. *F*-values are the test statistic for the difference between slopes (Snedecor and Cochran, 1980).

Table 3. Number (and percentage) of plants of *Pittosporum patulum* in four foliar stages (Fig. 2), eight height classes, and six diameter classes in northern and southern and forest and scrub populations. Height classes 1 = <1.0 m, 2 = 1.00–1.99 m, 3 = 2.00–2.99 m, 4 = 3.00–3.99 m, 5 = 4.00–4.99 m, 6 = 5.00–5.99 m, 7 = 6.00–6.99 m, 8 = >7.00 m. Diameter classes 1 = <3.0 cm, 2 = 3.0–7.9 cm, 3 = 8.0–19.9 cm, 4 = 20.0–54.9 cm, 5 = 55.0–149.9 cm, 6 = >150.0 cm.

Foliar class		1	2	3	4			
Northern	forest	109 (6)	271 (15)	51 (3)	19 (1)			
	scrub	3 (0)	20 (1)	24 (1)	5 (0)			
Southern	forest	258 (14)	435 (24)	75 (4)	105 (6)			
	scrub	54 (3)	128 (7)	103 (6)	155 (9)			
Height class		1	2	3	4	5	6	7	8
Northern	forest	153 (8)	155 (9)	89 (5)	37 (2)	9 (0)	4 (0)	2 (0)	0 (0)
	scrub	3 (0)	34 (2)	11 (1)	2 (0)	1 (0)	1 (0)	0 (0)	0 (0)
Southern	forest	330 (18)	283 (16)	122 (7)	61 (3)	24 (1)	32 (2)	14 (1)	6 (0)
	scrub	69 (4)	116 (6)	111 (6)	75 (4)	36 (2)	24 (1)	7 (0)	2 (0)
Diameter class		1	2	3	4	5	6		
Northern	forest	24 (1)	149 (8)	211 (12)	58 (3)	1 (0)	0 (0)		
	scrub	0 (0)	2 (0)	25 (1)	23 (1)	0 (0)	0 (0)		
Southern	forest	58 (3)	310 (17)	343 (19)	92 (5)	64 (4)	5 (0)		
	scrub	16 (1)	58 (3)	123 (7)	119 (7)	97 (5)	27 (1)		

as well as decreases in temperature, average rainfall, and rainfall:PET ratio (Fig. 4A). The demographic factors of stem height, stem diameter and age, and mean foliar stage increase along the axis from forest to scrub, while defoliation and dieback scores decrease (Fig. 4B).

The second major vegetation gradient is correlated with a southwest to northeast trend in the geographic coordinates of the plots. Solar radiation therefore increases significantly along the axis (Fig. 4A). Northern populations of west Nelson, Marlborough, and north Canterbury are broadly separated from those in south Canterbury and north Otago along this gradient (Fig. 3B). Tall silver beech forest communities containing *P. patulum* in the southern catchments (Communities D and E) have low Axis 2 scores, while species-poor subalpine scrub (Community F, present at Cobb Lake, Mt Patriarch and in the Clarence Valley as well as in south Canterbury) and mountain beech forests (Communities A and B) have high scores (Figs. 3A, B).

Demography

In total, we sampled 156 plots with *P. patulum* in 17 major river catchments in three broad regions: 7 (4.5%) in west Nelson, 69 (44.5%) in Marlborough and north Canterbury, and 80 (51%) in south Canterbury and north Otago. One hundred and seventy nine vascular plant species were recorded, including 172 in understorey tiers 5 and 6 (< 2 m) and 52 in height tiers > 2 m. The dataset contained a total of 1831 *P. patulum* plants. Stem height and stem diameter regression

relationships for the four foliar stages differ between forest and scrub associations for the northern and southern provenances (Fig. 5). The strongest separation is between the subadult and adult foliar stages; scrub populations show lower height relative to diameter for these two stages than forest populations in both provenances (Stages 3 and 4; Fig 5C, D, G, H). Stage 1 plants in scrub also show lower height relative to diameter in the southern provenance ($F = 3.96$ by t-test for difference between slopes, $P = 0.047$). The southern provenance also shows a greater average diameter than the northern population in both subadult (average northern 2.06 cm, southern 2.86 cm $F = 21.1$ by t-test, d.f. = 1, $P < 0.001$), and adult (average northern 3.30 cm, southern 8.31 cm, $F = 22.7$ by t-test, d.f. = 1, $P < 0.001$) foliar stages and greater height in the adult life stage (average northern 3.58 m, southern 4.18 m, $F = 22.7$ by t-test, d.f. = 1, $P = 0.021$). The seedling and sapling stages can attain particularly tall stem heights in forest.

The number and proportion of plants in the four foliar classes differs substantially between the northern and southern populations (Table 3). The southern population is much larger than the northern in all four foliar stages, but particularly in scrub communities. Together, subadults and adults account for far smaller proportions of plants in the north (19.7% in the north v. 33.4% in the south, $\chi^2 = 12.9$, d.f. = 1, $P < 0.001$); in particular, the number of older plants in the north is small (there are 24 adults compared with 260 in the south). The ratio of adults and subadults to seedlings and saplings in the northern provenance is 1:4.1, whereas it is 1:2 in the south. In both vegetation types,
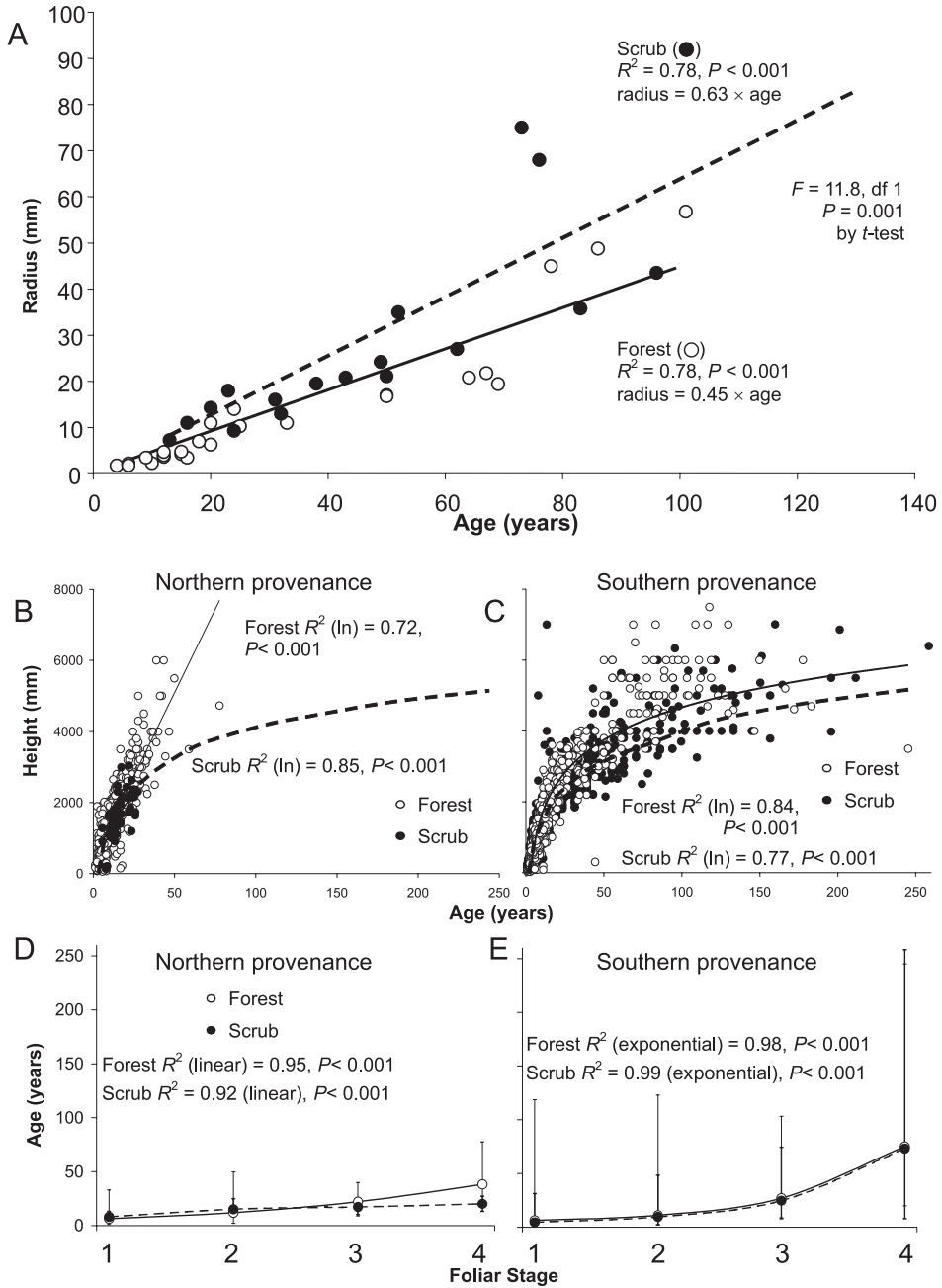
Figure 6. Age-related growth rates for *Pittosporum patulum*. A, radial increment growth rates of stems (*F*-value is the test statistic for the difference between slopes; Snedecor and Cochran, 1980); B and C, estimated height increment of stems, with estimated age from forest (open circles) and scrub (closed circles) and for northern and southern provenances (slopes are not significantly different between forest and scrub); estimated mean, maximum, and minimum ages for foliar stages in forest (open circles) and scrub (closed circles) associations in D, northern provenance and E, southern provenance. We show best fit regression relationships (solid for forest; scored for scrub) and *P*-value where probability of fit is significant. B-E relationships are based on radial increment growth rates from Fig. 6a.

stem diameter distributions are broadly unimodal in both provenances (Table 3). However, plants with stems in the two largest diameter classes are nearly absent in the northern provenance, whereas they form a substantial proportion of the total population in the southern provenance, particularly in scrub (i.e. there are significant differences between provenances in the distribution of plants across diameter classes; χ^2 = 36.9, d.f. = 7, $P < 0.001$, as well as foliar stage classes $\chi^2 = 70.8$, d.f. = 3, $P < 0.001$). Overall, forest populations have a much greater proportion of small diameter stems than do scrub populations (χ^2 = 294.6, d.f. = 5, $P < 0.001$). Height classes follow an inverse J-shaped distribution for forest, but are more unimodal for scrub in both provenances (Table 3).

Life span and growth rates

Assuming growth rings are annual, the oldest individual, a recently dead tree from the Huxley River, south Canterbury, was 130 years of age. Given the numerous dead leaf bases, this tree likely suffered premature death from herbivore browsing, with the likelihood that life expectancy for the species would exceed its 130 years. Radial increment growth rates from scrub (approximately 0.8 mm/year) mostly exceed those from forest (approximately 0.5 mm/year) throughout the range of stem diameters (Fig. 6A). As trees age, they show increasing variability in radial increment growth rates, with some individuals in scrub growing particularly rapidly. Estimated height extension growth rates of stems are slightly greater in forest than in scrub for both provenances (Fig. 6B, C). Mean vertical growth rates from cut discs of stem wood from forest (122.2 ± 86.3 mm/year) exceeded those from scrub (68.7 ± 59.2 mm/year). The mean predicted ages at each of the four foliar stages are broadly similar for forest and scrub in both the northern and southern provenances (Fig. 6D, E). However, the maximum and minimum predicted confidence limits of plant age are greater for forest than for scrub, especially in foliar stages 3 and 4.

Relationship between defoliation, dieback, and demography

Defoliation and dieback scores for *P. patulum* are associated with and significantly correlated with demographic measures across the entire dataset and inconsistently with forest and scrub in the northern and southern provenances (Table 4). Specifically, defoliation is negatively related with foliar stage (R^2 = 0.017, d.f. = 1, $P < 0.001$), stem height (R^2 = 0.004, d.f. = 1, P = 0.005), and stem diameter (R^2 = 0.007, d.f. = 1, $P < 0.001$) for the entire dataset, and with foliar stage in both provenances (northern R^2 = 0.013, d.f. = 1, P = 0.009; southern R^2 = 0.020, d.f. = 1, $P < 0.001$).

However, defoliation relationships are not consistently negative; in a few catchments and sub-catchments, defoliation was positively correlated with foliar stage, stem height, and stem diameter. Overall, there were more associations and correlations between defoliation and foliar stage, stem diameter, and stem height for forest than for scrub (Table 4). Dieback was frequently associated and generally positively correlated with foliar stage, stem height, and stem diameter for the entire dataset, both provenances, and in many catchments and sub-catchments. However, dieback was not associated or correlated with stem height in scrub populations in either provenance. Of the trees with heavy defoliation (defoliation class 4), the highest proportions were in foliar stages 2 (42% of heavily defoliated plants) and 1 (33% of heavily defoliated plants) (Table 5). Defoliation and dieback are strongly positively associated across the entire dataset, in the two provenances, and in several catchments and sub-catchments (Table 4).

Symptoms of defoliation

The frequency of defoliation symptoms was not systematically recorded. However, evidence of defoliation by brushtail possums was common and similar to those on other broad-leaved species — much of the leaf lamina is removed leaving a torn, jagged edge of coarse, irregular serrations or, commonly, just a decapitated petiole. Browse sign on leaves above *c.* 2.5 m in height and on any part of cliff plants was sporadic and resulted from possums alone. Judging by the uniform age of damage, some subadult and adult plants had been heavily or completely browsed within a narrow timeframe that they may not recover from. Possums are also likely to be the main agent for chewed bark and cambium, which was sporadic on subadults and adults. Symptoms of insect damage to leaves appeared in many populations as partial loss of the lamina, with a more finely serrated and regular margin than the irregular edge of possum browse. Decapitated stems of seedlings and saplings in many northern provenance populations resulted from lagomorphs and ungulates, as well as possums. Overall, possum browse was the most widespread and abundant damage, although decapitated stems of seedlings and saplings were frequent in *Nothofagus* forest understoreys.

Discussion

Distribution

There is no ready environmental (LENZ) explanation for the absence of *Pittosporum patulum* from western mid-Canterbury. Further, the model predictions for the

Table 4. Relationships between defoliation, dieback and demographic features of *Pittosporum patulum*, for the entire dataset, northern and southern provenances, and those catchments and sub-catchments containing >15 plants. We show significant chi-squared values (where expected >5 plants for each cell in the contingency table), and the direction and percent variation explained (R^2%) of significant linear relationships between variables. Foliar stage, stem height, and stem diameter classes or categorical variables were used in the chi-squared tests and continuous height and diameter data were used for the regressions (foliar stage was treated as a continuous variable for regression analysis). Numbers of sampled plants for provenances and major catchments are shown in parentheses. ns = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$ (all Bonferroni corrected for multiple tests); – = number of plants insufficient for chi-squared test.

| Character | Defoliation (score 0–4) | | | | | | Dieback (score 0–4) | | | | | | Defoliation Dieback |
| | Foliar stage | | Stem height | | Stem diameter | | Foliar stage | | Stem height | | Stem diameter | | |
Test	χ^2	R^2%	χ^2	R^2%	χ^2	R^2%	χ^2	R^2%	χ^2	R^2%	χ^2	R^2%	χ^2
TOTAL	58	–2**	78***	–1***	95***	–1***	18*	ns	52***	1***	88***	9***	354***
Forest (1340)	34***	ns	84***	ns	84***	ns	57***	1**	107***	6***	142***	9*	217***
Scrub (500)	ns	ns	ns	ns	ns	ns	24**	–2***	ns	ns	42***	ns	119***
NORTHERN (520)	ns	–1**	29*	ns	ns	ns	35***	ns	40**	3***	39***	5***	124***
Forest (464)	ns	–1*	ns	ns	ns	ns	30***	ns	41**	4***	42***	6***	90***
Scrub (56)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	42***
Cobb River (65)	–	ns	–	ns	–	ns	–	ns	–	32*	–	40**	-
Mt Patriarch (133)	–	ns	–	ns	–	18*	–	ns	–	ns	–	ns	70***
Travers River (22)	–	ns	–	ns	–	ns	–	ns	–	54**	–	51*	–
Wairau River (48)	–	ns	–	ns	–	ns	–	ns	–	ns	–	ns	–
Lake Tennyson (42)	–	ns	–	ns	–	ns	–	ns	–	ns	–	ns	–
Boyle River (123)	–	ns	–	ns	–	ns	–	26**	–	35***	–	41***	–
Hope River (16)	–	ns	–	ns	–	ns	–	ns	–	ns	–	ns	–
Hurunui River (28)	–	ns	–	ns	–	ns	–	ns	–	ns	–	49*	–
Cox River (41)	–	ns	–	ns	–	ns	–	ns	–	ns	–	ns	–
SOUTHERN (1320)	61***	–2***	68***	1**	84***	–1***	29***	ns	51***	2***	69***	1***	273***
Forest (876)	29**	ns	71***	ns	67***	6*	59***	3***	94***	7***	120***	10***	172***
Scrub (444)	19*	ns	35*	ns	ns	ns	38***	–2***	ns	ns	33**	ns	51***
Tasman River (84)	–	ns	–	ns	–	ns	–	ns	–	ns	–	ns	–
Dobson River (184)	ns	ns	–	ns	ns	ns	ns	ns	42**	21**	ns	23**	29***
Hopkins River (807)	34***	–2***	47*	ns	47***	ns	33***	ns	38*	1*	84***	1*	358***
Ahuriri River (52)	–	–33*	–	ns	–	ns	–	ns	–	ns	–	ns	–
Dingle Burn (193)	–		–	ns	–	ns	–	ns	–	ns	–	ns	–
Hopkins sub-catchments													
Elcho Stream (41)	ns	ns	ns	ns	ns	ns	19*	ns	22*	11*	42*	24**	ns
Huxley River (27)	–	18*	–	ns	–	ns	–	ns	–	ns	–	ns	–
Maitland Stream (56)	26*	ns	53**	13**	33**	20***	30***	24***	56***	51***	53***	58***	35***
North Elcho Stream (11)	–	ns	–	ns	–	ns	–	ns	–	ns	-	ns	-
North Huxley Stream (146)	27**	ns	ns	ns	23*	ns	20*	7**	80***	14***	35***	16***	35***
North Temple Stream (118)	ns	ns	ns	–4*	ns	ns	21*	ns	ns	–7*	30**	–3*	77***
South Elcho Stream (5)	–	ns	–	ns	–	ns	–	ns	–	ns	–	ns	–
South Huxley Stream (5)	–	ns	–	–86*	–	ns	–	ns	–	ns	–	ns	–
South Temple Stream (370)	17*	–1*	ns	ns	ns	ns	23***	–3*	ns	ns	33**	ns	194***
Unnamed stream (28)	–	ns	–	ns	–	ns	–	30**	–	19*	–	32**	–

Table 5. Number and percentage of stems by foliar stage in four defoliation classes for northern and southern provenances of *Pittosporum patulum.*

Provenance	Northern				Southern			
Foliar stage	1	2	3	4	1	2	3	4
Defoliation class								
1	53 (47)	169 (58)	40 (53)	18 (75)	134 (44)	242 (46)	64 (52)	96 (49)
2	31 (28)	67 (23)	24 (32)	5 (21)	81 (26)	139 (26)	33 (27)	69 (35)
3	13 (12)	35 (12)	4 (5)	0 (0)	54 (18)	107 (20)	8 (7)	19 (10)
4	15 (13)	18 (6)	7 (9)	1 (4)	36 (12)	49 (9)	18 (15)	14 (7)
Total	112	289	75	24	305	537	123	198

Tararua and Ruahine Ranges seem untenable in terms of thorough previous botanising there, whereas those for the Inland and Seaward Kaikoura Ranges are more plausible in this extensively deforested zone. Significantly, the model shows no potential extension onto the west side of the Southern Alps. Besides lower solar radiation in the south, no climatic contrasts can be seen between the two provenances or between the provenances and the central 'gap'. Overall, the poor concordance between its present range and that predicted by LENZ suggests that: 1) the LENZ variables provide inadequate physiographic modelling and others such as soil N might be important, 2) that biotic factors such as competition are influential, and 3) that earth history such as a sluggish re-colonisation of range vacated in the last glaciation is influential in its distribution.

There is only the broadest concordance between the *P. patulum* gap and the Canterbury beech (*Nothofagus*) gap (Wardle, 1984; Wardle, 1991: Fig. 7.25). Indeed, the Canterbury beech gap is problematic compared to the equivalent mid-Westland gap on the opposite side of the Southern Alps (Wardle, 1984) because (1) extensive deforestation has obliterated the pre-human community pattern and removed virtually all forest in the major headward catchments and (2) some forest remnants are fire-modified and secondary. The northern boundaries of the two gaps have poor agreement, with *P. patulum* limits in the northern tributaries of the Waimakariri River headwaters and scattered beech south of this through the Rakaia and Ashburton rivers to the Rangitata River headwaters. There is, however, strong concordance in the reappearance of both groups on the southern side of their gaps — both appear on the southern flanks of the basin drained by the Tasman River and Lake Pukaki.

Habitat and regeneration

Habitat preferences and regeneration modes can be interpreted from the plot-based geographic and demographic data. Within *Nothofagus* forest, environmentally stressed microsites such as the inverted treeline of valley floors, the thin soils along the margins of steeply-incised stream courses and around rock bluffs, and the poorly drained soils of shallow depressions on benches all suppress the height and closure of a *Nothofagus* canopy. Adult plants were almost always found in the above microsites that appeared to provide light environments superior to those of the surrounding *Nothofagus* forest understoreys and presumably sufficient for *P. patulum* to reach reproductive maturity. Given that etiolated subadults are usually the oldest individuals within treefall gaps, gap closure rates probably preclude adulthood within forest. Average height growth rates for *Nothofagus solandri* span 300–600 mm/year and for *N. menziesii* 300–400 mm/year (Wardle, 1984: 287–288), considerably greater than those for *P. patulum* from the present study. The inverse J-shaped size-class distribution in forest points to continuous recruitment in its environmentally stressed microsites.

Its patchy occurrence and broadly unimodal diameter and foliar stage demography in scrub suggests pulsed recruitment. Larger scale disturbances such as snow and debris avalanche, cyclonic wind-throw and fire would create secondary woody successions at scales and at rates of change compatible with a cohort of *P. patulum* reaching reproductive maturity. Such disturbances create both seral scrub within the forest zone and influence the dynamics of subalpine scrub above the forest or in the cold heads of valleys.

Van Eyndhoven and Norton (2001) suggest disturbance is critical for regeneration. However, we downplay disturbance as a recruitment stimulus in forest, pointing instead to permanent light-gaps from climatic or edaphic stress as its reproductively-successful habitat. Alternatively, landscape-scale disturbance may explain its unimodal demography and patchy distribution in scrub, although our demographic sample may be biased by the difficulty of detecting juveniles in scrub thickets.

Seed dispersal

Flowers and fruit were recorded in few populations,

partly because adults are rare in the northern provenance and perhaps because adults may reproduce inconsistently (e.g. Schauber *et al.*, 2002). Seeds mature within a two-valved, fleshy green capsule. In this state, seeds have a fleshy, succulent testa, presumably offering a fruit sugar reward for dispersal. Birds are likely to be the main seed dispersal vector, either deliberately consuming the succulent seed within green capsules or inadvertently, with the sticky dried seeds attached to feathers after the capsules dehisce. Triangular puncture marks the size of a bellbird (*Anthornis melanura*) or blackbird (*Turdus merula)* bill in green and unopened capsules point to a frugivorous bird-vector for the succulent seed. However, ripe capsules and their succulent seed, both on trees and within ground litter, appeared to be heavily preyed on by rodents, judging by the fracture pattern of damaged capsules. Possums also probably consume capsules and seed.

With few adults in the north and potentially just half producing seed [(*P. patulum* is dioecious (Godley in Cooper, 1956), although a small proportion of 'male' plants occasionally produce female flowers and a few seed capsules ('inconstant males' of Godley, 1979; see also Clarkson and Clarkson, 1994)], most northern populations may have reached a reproductive bottleneck. Compromised seed production and dispersal for a species partly reliant on within- and between-catchment transport to exploit a shifting mosaic of disturbance-induced clearings of successional scrub within forest or subalpine scrub are important questions remaining from this preliminary investigation.

Herbivory

Although we have no historical demographic data to compare with the present study, the present variable but often high levels of defoliation and proportionately low numbers of subadults and adults in the north point to *P. patulum* being threatened by pest herbivory (Table 2, 3, & 5). Further, the evidence is that defoliation leads to advancing dieback as trees increase in size and maturity. Although, defoliation reduces with advancing foliar stage, stem height, and stem diameter across the entire dataset, this relationship is not consistent in the northern and southern provenances and in forest and scrub vegetation (Table 4). Reducing defoliation with plant maturity suggests that herbivore impacts reduce as plants grow beyond the reach of the ground-based pests (deer, goats, hares and possums), with possums remaining as the only arboreal browser. The analysis also suggests that the species is more vulnerable to defoliation in forest than scrub, although the bulk of the biomass in both communities is of low dietary appeal to possums (Owen and Norton, 1995; Nugent *et al.*, 1997; Nugent *et al.*, 2000). There are no consistent

differences in *P. patulum* abundance, size, defoliation or dieback to point to differential vulnerability to pests in mountain as opposed to silver beech-dominated communities (Table 2).

There is an alternative explanation for the species' broadly unimodal foliar stage distributions (Table 5) to that offered by pulsed recruitment, which would apply equally to the significantly greater percentage of heavily defoliated trees in foliar stages 1 and 2. We suggest that the younger life stages are vulnerable to a suite of terrestrial pests, whereas the adults are preferred by possums. Etiolated saplings may escape defoliation because their foliage exceeds the reach of ungulates and their stems have insufficient rigidity to support browsing possums. Further, a proportion of adults appear to be susceptible to one-off, heavy defoliation events producing a patchy dieback pattern within some southern stands.

Although bereft of subadults and adults, many northern populations have abundant juveniles. Three possible explanations are that: (1) present-day seedlings and saplings result from delayed germination of a litter and soil seed source; (2) stem radial and vertical growth rates are extremely slow and juvenile size classes have a shade-induced, semi-dormant state; (3) reproducing adults remain undetected.

We dismiss the last one as improbable, in the knowledge of the intensive botanical surveillance of many *P. patulum* catchments in Nelson–Marlborough in the last three decades. There is some support for the first explanation in a *c.* 2-year delay in seed germination in nursery trials, with germination in the wild possibly responding to environmental triggers after the disappearance of adults (see also van Eyndhoven and Norton, 2001). For example, in three nursery trials between 1998 and 2001, seed germinated 17–18 months after sowing (N. Simpson, Conservation Consultancy Ltd, Queenstown *pers. comm.*, 2000; J. Santos, Department of Conservation, Motukorara *pers. comm.*, 2001; J. Barkla, Department of Conservation, Dunedin *pers. comm.*, 2002). Support for the second explanation is the slow radial growth rate of stems in forest understoreys (Fig. 6).

There are particularly low numbers of *P. patulum* in northern scrub communities compared with those of the south. The first explanation is that this community has had a differentially long history of pest herbivory. Possums are recent invaders and probably still at pre-peak densities in the headward catchments of the South Canterbury's lakes district, whereas they have a long history of colonisation of *P. patulum*'s Nelson–Marlborough range (Cowan, 1990; Clout and Ericksen, 2000). Red deer have a similar colonisation history in the two provenances (Challies, 1990). We have no observations or data for goats or hares. Southern-most Community H has the greatest average defoliation and

the least dieback, implying a short history of pest occupancy. An alternative explanation is that the irregular *Nothofagus* treelines and abrupt transitions from forest to tussockland testify to the disruptive influence of fire in summer-dry Marlborough.

Further, adult foliage, often with seed capsules, is prominent in CHR herbarium vouchers from Nelson and Marlborough until the 1970s. However, all specimens collected since are of seedling and sapling foliage. Druce (in Eagle, 1982:269) noted that "adult plants were very hard to find" in Nelson–Marlborough in the 1970s, as did J. Hayward in 1991 (File note PES:265, Department of Conservation, Renwick, Marlborough). Further, a monitored population separate from this study also suggests pest herbivore-induced decline: between 1985 and 1991 along the Lake Chalice–Patriarch Ridge, Richmond Range, Marlborough, 14 % of monitored *P. patulum* seedlings and saplings suffered decapitated tops and were dead or dying (File note PES:265, Department of Conservation, Renwick, Marlborough).

Conservation strategy

Although distributed widely, *P. patulum* is locally frequent but never abundant because its specialist habitat requirements (to reach reproductive maturity) are sparsely distributed within *Nothofagus* forest. Particularly across the northern provenance, its geographic and local demographic viability is threatened by low numbers of adults, heavy defoliation across all foliar stages, and many populations occupying shaded forest understoreys with no prospects of reaching reproductive maturity. Given the evidence for a reproductive 'bottleneck' in the north and moderate to high levels of defoliation throughout its range, we agree with the 'nationally endangered' conservation threat ranking of de Lange *et al.* (2004) (based on the estimated number of mature individuals and their assumed rate of decline of ≥ 30% over the last 100 years). Our community classification and ordination could underpin an objective conservation strategy for *P. patulum*, covering representative vegetation types and environments, potentially covering the full ecological and/or genetic range of the species.

Finally, because we make inferential judgements on aspects of the species' ecology and conservation status, we recommend that a protection strategy should test, perhaps using factorial experiments, the reproductive bottleneck hypothesis in terms of:

1. Reproductive potential in different forest understorey light-environments spanning canopy-gaps, both edaphic and disturbance-induced, and non-gaps;
2. Hares, ungulates, and possums as potential pest herbivores at different life stages of the plant using exclosure treatments.

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References

Allen, R.B. 1992. *An inventory method for describing New Zealand vegetation*. Forest Research Institute Bulletin No. 181. Ministry of Forestry, Christchurch, N.Z.

Challies, C.N. 1990. Red deer. *In:* King, C.M. (Editor), *The handbook of New Zealand mammals*, pp. 436-458. Oxford University Press, Auckland, N.Z.

Clarkson, B.D.; Clarkson, B.R. 1994. Ecology of an elusive endemic shrub, *Pittosporum obcordatum* Raoul. *New Zealand Journal of Botany 32:* 155-168.

Clifford, H.T.; Stephenson, W. 1975. *An introduction to numerical classification*. Academic Press, New York, U.S.A.

Clout, M.; Ericksen, K. 2000. Anatomy of a disastrous success: the brushtail possum as an invasive species. *In:* Montague, T.L. (Editor), *The brushtail possum: biology, impact and management of an introduced marsupial*, pp. 1-9. Manaaki Whenua Press, Lincoln, N.Z.

Cooper, R.C. 1956. The Australian and New Zealand species of *Pittosporum. Annals of the Missouri Botanical Garden 43:* 87-188.

Cowan, P.E. 1990. Brushtail possum. *In:* King, C.M. (Editor), *The handbook of New Zealand mammals*, pp. 68-98. Oxford University Press, Auckland, N.Z.

de Lange, P.J.; Norton, D.A.; Heenan, P B.; Courtney, S.P.; Molloy, B.P.J.; Ogle, C.C.; Rance, B.D.; Johnson, P.N.; Hitchmough, R. 2004. Threatened and uncommon plants of New Zealand. *New Zealand Journal of Botany 42:* 45-76.

Dopson, S.R.; de Lange, P.J.; Ogle, C.C.; Rance, B.D.; Courtney, S.P.; Molloy, J. 1999. *The conservation requirements of New Zealand's nationally threatened vascular plants*. Threatened Species Occasional Publication No. 13. Department of Conservation, Wellington, N.Z.

Eagle, A. 1982. *Eagle's trees and shrubs of New Zealand*. Collins, Auckland, N.Z.

Environmental Systems Research Institute 2000. *ArcView GIS: The geographic information system for everyone*. Environmental Systems Research Institute, Redlands, California, U.S.A.

Godley, E.J. 1979. Flower biology in New Zealand. *New Zealand Journal of Botany 17:* 441-466.

Hill, M.O.; Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio 42:* 47-58.

Joyce, L. 1993. (unpublished). *Animal browse of* Pittosporum patulum *seedlings: Chalice-Patriarch ridge, north-west Nelson*. Diploma in Wildlife Management thesis, University of Otago, Dunedin, N.Z.

Leathwick, J.R.; Wilson, G.; Rutledge, D.; Wardle, P.; Morgan, F.; Johnson, K.; McLeod, M.; Kirkpatrick, R. 2003. *Land environments for New Zealand*. David Bateman, Auckland, N.Z.

Lillie, A.R. 1980. *Strata and structure in New Zealand*. Tohunga Press, Auckland, N.Z.

New Zealand Geological Survey 1972. South Island (First edition), *Geological Map of New Zealand 1:1 000 000*. Department of Scientific and Industrial Research, Wellington, N.Z.

Nugent, G.; Fraser, K.W.; Sweetapple, P.J. 1997. *Comparison of red deer and possum diets and impacts in podocarp-hardwood forest, Waihaha catchment, Pureora Conservation Park*. Science for Conservation 50. Department of Conservation, Wellington, N.Z.

Nugent, G.; Sweetapple, P.; Coleman, J.; Suisted, P. 2000. Possum feeding patterns: dietary tactics of a reluctant folivore. *In:* Montague, T.L. (Editor), *The brushtail possum: biology, impact and management of an introduced marsupial*, pp. 10-23. Manaaki Whenua Press, Lincoln, N.Z.

Owen, H.J.; Norton, D.A. 1995. The diet of introduced possums *Trichosurus vulpecula* in a low-density New Zealand *Nothofagus* forest and possible implications for conservation management. *Biological Conservation 71:* 339-345.

Payton, I.J.; Pekelharing, C.J.; Frampton, C.M. 1999. *Foliar browse index: a method for monitoring possum (*Trichosurus vulpecula*) damage to plant species and forest communities*. Manaaki Whenua-Landcare Research, Lincoln, N.Z.

Rogers, G.M.; Walker, S. 2002. Taxonomic and ecological profiles of rarity in the New Zealand vascular flora. *New Zealand Journal of Botany 40:* 73-93.

Schauber, E.M.; Kelly, D.; Turchin, P.; Simon, C.; Lee, W.G.; Allen, R.B.; Payton, I.J.; Wilson, P.R.; Cowan, P.E.; Brockie, R.E. 2002. Masting by eighteen New Zealand plant species: The role of temperature as a synchronising cue. *Ecology 83:* 1214-1225.

Snedecor, G.W.; Cochran, W.G. 1980. *Statistical methods*. Seventh edition. Iowa University Press, Ames, Iowa, U.S.A.

van Eyndhoven, E.; Norton, D.A. 2001. Habitat characteristics, population structure, and regeneration strategy of the endangered small tree *Pittosporum patulum*. *Canterbury Botanical Society Journal 35:* 54-65.

Wardle, J.A. 1984. *The New Zealand beeches: ecology, utilisation, and management*. New Zealand Forest Service, Wellington, N.Z.

Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge. U.K.