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# VEGETATION AND SOIL RECOVERY ON SHALLOW LANDSLIDE SCARS IN TERTIARY HILL COUNTRY, EAST CAPE REGION, NEW ZEALAND

**Summary:** Primary successions involving teatree (*Kunzea ericoides* var. *ericoides* with some *Leptospermum scoparium*) were studied on shallow landslide scars on soft sedimentary (mudstone) hill country under extensive pastoral use in the East Cape (Tairawhiti) region, using a 5-72 yr chronosequence established from sequential aerial photography and the age of the oldest teatrees on scars. Dynamics of primary even-aged teatree stands are similar to those in secondary successions on reverting pasture described previously from the region. Height growth rates and basal area indicate that the productivity of teatree stands on landslide scars is similar to that on intact regolith. Although seventy five vascular species were recorded, one-third of them adventive, only five species - all native - were consistently present. Classification and ordination revealed four distinct stages in the evolution of ground layer communities, the first three with <50% plant cover (establishment and persistence of adventive grasses and herbs for 15 years; exclusion by shading of species other than *Hypochoeris radicata* and mosses from 15-30 years; establishment of *Microlaena stipoides, Uncinia* spp., and ferns from 30-50 years) and the fourth with >50% plant cover (principally *M. stipoides*, from 50 years), reflecting the dynamics - dominated by intraspecific competition - of the teatree stands. Apart from *Leucopogon fasciculatus*, other early successional canopy species were rare and later successional canopy species typical of primary forest in the region were absent. Despite the presence of seed sources of later successional canopy species in nearby remnants of primary forest and the persistence of their dispersers, continued removal of mostly palatable potential successors by grazing will stall their progression to tall forest. Mean soil depth increased logarithmically with age, from an average of 20 cm at age 10 yr to 58 cm at age 70 yr, a rate substantially faster than on sandstone elsewhere in the country.

**Keywords:** kanuka; *Kunzea ericoides*; primary succession; soil depth; landslide scars; East Cape; North Island; New Zealand.

## Introduction

Soil erosion on the soft sedimentary hill country of the East Cape (Tairawhiti) region has accelerated greatly since the removal around a century ago of most of the original tall forest cover for agriculture, with adverse social and economic effects (*e.g.*, loss of agricultural productivity) both on- and off-site. In the past 20 years substantial areas have been re-afforested with exotic *Pinus radiata* D. Don. in an attempt to reverse this trend. Elsewhere, invasion of extensively grazed pasture by teatree - mostly kanuka, *Kunzea ericoides* var. *ericoides* (A. Rich.) J. Thompson, with some manuka, *Leptospermum scoparium* J.R. et G. Forst., in places - occurs widely where seed sources of these species are present (Bergin, Kimberley and Marden, 1995) and may foreshadow eventual reversion to tall forest in the absence of intervention. Kanuka is a widespread precursor of tall forest of New Zealand, forming steady-state communities only in the driest parts of the country (e.g., Burrell, 1965). Teatree, particularly kanuka, is also the major primary coloniser of erosion scars in extensively grazed pasture in the region; these are formed mostly by landsliding, the commonest form of erosion in the lowland steeplands ('hill country') of New Zealand (Blaschke, Trustrum, and de Rose, 1992).

Previous studies on sedimentary hill country elsewhere on the east coast of the North Island showed an exponential recovery of annual pasture production after slipping, occurring mostly over the first 20 years but, in the Wairarapa at least, apparently unlikely to return to previous levels for a century or more (Lambert, Trustrum, and Costall, 1984; Douglas, Trustrum and Brown, 1986). Primary vegetation successions on landslide scars and relationships between soil depth and landslide age have been modelled on somewhat similar lithology in inland Taranaki (Blaschke *et al.,* 1992; Trustrum and de Rose, 1988). In this study we examined vegetation and soil on shallow translational landslide scars of a variety of ages in extensively grazed parts of the region, in order to determine patterns of primary succession involving natural vegetation, and rates of soil recovery after mass movement. Most of the scars studied were located within tracts of secondary teatree scrub and forest.

# Methods

## Study areas

Seven study areas were used, one in the Turanganui River catchment, three in the lower Waipaoa River catchment and three in the Tolaga Bay catchment; all are in the lowland bioclimatic zone (Fig. 1). Apart from the Turanganui catchment (recent marine sediments), all are on mudstone of Tertiary age (O'Byrne, 1967). Soils are well drained Recent Orthic Weathered or Typic soils (Hewitt, 1992) on steep slopes. Climate is mild and humid, with a mean annual rainfall of 1200-1600 mm falling on about 120 days, and a marked winter maximum. Summer drought is a marked feature of the climate. Mean annual temperature is 13-15°C, with a mean midsummer (January) temperature of 18-19°C and a mean midwinter (July) temperature of 8-10°C (New Zealand Meteorological Service, 1985). Winds overall have a slight, strong winds a marked north-westerly predominance (Tomlinson, 1976).

## Data collection

Twenty four individual landslide scars in extensively grazed reverting pasture were identified from sequential aerial photography. Shallow translational landslides tend to have a clearly definable morphology, with an overall spoon shape (Schuster and Krizek, 1978), a nearly vertical arc-shaped 'headwall' and a less distinct 'debris tail'. Scars on upper faces were chosen in preference to those lower down where subsequent deposition of rafted material was likely to have occurred.

In the absence of time-series data from permanent plots, temporary rectangular plots of

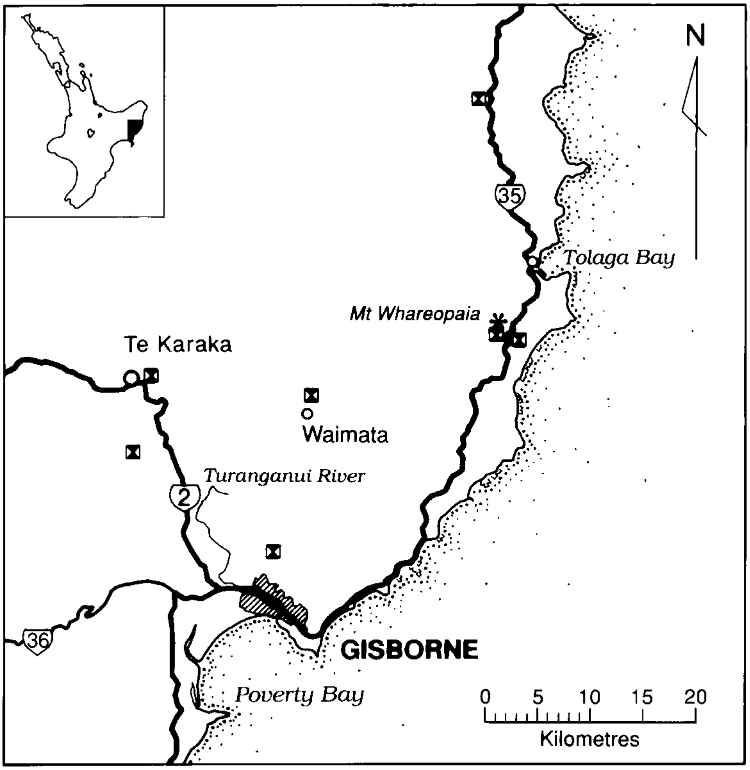


Figure 1: *Location of the study areas.*

variable area but sufficiently large to include at least 15 canopy individuals were placed on landslide scars of various ages, one per scar, avoiding headwalls and debris tails. Plot area ranged from 0.001 to 0.006 ha. In each plot, slope and aspect were recorded along with diameter at 1.4 m above ground (breast height) of all trees >2.5 cm dbh, living and dead. Seedlings (<2.5 cm dbh) >15 cm high were counted. Ground cover was estimated by species semi-quantitatively in seven classes (<1, 1-5, 5-25, 25-50, 50-75, 75-95, >95%). At least three teatree plants - covering the diameter range of the stand - were felled and measured for height. Basal discs were removed, sanded, and aged; rings were assumed to be annual. The oldest teatree on each landslide scar was assumed to represent the minimum age of the scar.

Soil depth was measured at fifteen of the same sites by inserting an 18 mm diameter cone-tipped probe into the soil until it contacted the relatively unweathered underlying mudstone. Measurements were made normal to the slope on a 1 m grid across each landslide scar. The study location in the Turanganui River catchment was not sampled for soil depth because of differing parent material (marine sediments *cf.* mudstones).

***Analysis***

Exponential chronofunctions of the form

$$y = a\,(1-b^{Age})$$

were fitted for y = height (m) of tallest teatree in the stand and for y = diameter (cm) of the teatree of mean basal area, where

$$Age = \text{plot age (yr)},$$

and a and b are constants. For both height and diameter linear models gave fits which were almost as good. An inverse square function of the form

$$Den = a.Age^{-2}$$

was fitted where Den = density of teatree individuals per hectare, a is a constant and Age = plot age (yr). Ground cover scores were classified using TWINSPAN (Hill 1979a) and ordinated using DECORANA (Hill 1979b). The significance of differences between ages of communities identified by TWINSPAN classification were tested by ANOVA. A logarithmic function of the form

$$\text{Soil depth} = a + b.\,\log_{10}(Age)$$

was fitted, where a and b are constants.

# Results

## Vegetation development

***Species composition***

Seventy-five vascular plants were recorded in plots, of which one-third were adventive (Table 1); all are common and widespread in the region. Nearly two-thirds were 'accidentals', occurring in only one or two plots. Apart from kanuka only four species - twiggy coprosma (*Coprosma rhamnoides* A. Cunn.), catsear (*Hypochoeris radicata* L.), meadow rice grass (*Microlaena stipoides* (Lab.) R. Br.), and hook-sedges (mostly *Uncinia uncinata* (Linn. f.) Kuek.) - were consistently present, *i.e.*, in more than half the plots. Woody plants - especially shrubs - and ferns constituted the bulk of the native species and dicotyledonous herbs most of the adventives.

***Teatree population structure***

The range of ages in the samples within individual stands varied from 1 to 29 years and was significantly ($P$<0.05) though weakly ($r^2$ = 0.21) correlated with stand age, *i.e.*, older stands tended to have a wider age range. The age range was biased towards the lower end, however, over half the stands having a range of less than 7 years. All but one stand was even-aged (see Smith, 1962).

Diameter frequency distributions (Fig. 2) for seven stands representing the age range present show a gradual progression from an 'reverse J' shape up to age approx. 30 years to a more bell-shaped distribution by age 45 years. Where present, dead manuka plants constituted 18% of the population in a 14-yr-old stand and between 53% (50 yr) and 88% (33 yr) of the population elsewhere. Dead kanuka accounted for between 10% (38 yr) and 33% (30 yr) of the population. In three of the four stands with dead manuka present, the average diameter of dead plants was slightly smaller than that of live ones (85%), while in the four stands with dead kanuka present, the average diameter of dead plants was much smaller (29%) than that of live ones. In three of the four stands where both species were present, the average diameter of live manuka was 26% that of kanuka.

***Mean diameter* vs *age***

The relationship between mean diameter (MD) and age is best described by the exponential function

$$MD = 628(1\text{-}0.999^{Age}),\ r^2 = 0.88$$

Mean annual diameter growth rate over all plots, indicated by linear regression ($r^2$ = 0.88, $P$<0.01, n = 24),was 0.31 cm $yr^{-1}$.

Table 1: *Vascular flora of primary successional teatree stands (5-72 yr old) on shallow landslide scars on Tertiary mudstones in the East Cape region. Percentage frequency of occurrence in younger (<37 yr) and older (>37 yr) stands. * denotes adventive*

| | Younger (n=11) | Older (n=13) |
|---|---|---|
| **Ferns** | | |
| *Adiantum cunninghamii* Hook. | 14 | 40 |
| *Asplenium terrestre* Brownsey | 7 | 0 |
| *Blechnum* sp. 1 (Brownsey and Smith-Dodsworth 1989) | 0 | 10 |
| *Cyathea dealbata* (Forst. f.) Swartz | 21 | 40 |
| *C. medullaris* (Forst. f.) Swartz | 14 | 0 |
| *Paesia scaberula* (A. Rich.) Kuhn | 0 | 10 |
| *Pellaea rotundifolia* (Forst. f.) Hook. | 0 | 10 |
| *Phymatosorus pustulatus* (Forster f.) Large emend Large, Braggins & Green | 7 | 0 |
| *Polystichum richardii* (Hook.) J. Smith | 7 | 70 |
| *Pteridium esculentum* (Forst. f.) Ckn. | 0 | 10 |
| *Pteris tremula* R. Br. | 21 | 0 |
| *Pyrrosia eleagnifolia* (Bory) Hovenkamp | 14 | 10 |
| **Dicotyledonous trees and shrubs** | | |
| **Berberis glaucocarpa* Stapf | 0 | 20 |
| *Carmichaelia cunninghamii* Raoul | 0 | 10 |
| *Carpodetus serratus* J.R. et G. Forst. | 7 | 0 |
| *Cassinia leptophylla* (Forst. f.) R. Br. s.l. | 14 | 0 |
| *Coprosma areolata* Cheeseman | 0 | 20 |
| *C. rhamnoides* A. Cunn. | 64 | 100 |
| *C. rigida* Cheeseman | 0 | 40 |
| *C. robusta* Raoul | 0 | 10 |
| *Coriaria arborea* Lindsay | 7 | 0 |
| **Cupressus* sp. | 0 | 10 |
| *Gaultheria antipoda* Forst. f. | 7 | 10 |
| *Geniostoma rupestre* Forst. et Forst. f. | 0 | 10 |
| *Hoheria sexstylosa* Col. | 0 | 10 |
| *Kunzea ericoides* var. *ericoides* (A. Rich.) J. Thompson | 100 | 100 |
| *Leptospermum scoparium* J.R. et G. Forst. | 43 | 20 |
| *Leucopogon fasciculatus* A.Rich. | 43 | 40 |
| *Macropiper excelsum* (Forst. f.) Miq. | 0 | 10 |
| *Melicytus ramiflorus* ssp. *ramiflorus* J.R. et G. Forst. | 7 | 10 |
| *Myrsine australis* (A. Rich.) Allan | 7 | 10 |
| *Olearia rani* (A. Cunn.) Druce | 0 | 10 |
| *Pittosporum tenuifolium* Sol. ex Gaertn. s.s. | 0 | 10 |
| *Pseudopanax crassifolius* (Sol. ex A. Cunn.) C. Koch | 7 | 10 |
| *Sophora tetraptera* J. Mill. | 7 | 0 |
| **Dicotyledonous lianes** | | |
| *Calystegia tuguriorum* (Forst. f.) R.Br. ex Hook. f. | 0 | 10 |
| *Clematis paniculata* Gmel. | 14 | 20 |
| *Parsonsia* sp. | 0 | 10 |
| *Rubus cissoides* A. Cunn. | 14 | 10 |
| **Dicotyledonous herbs** | | |
| *Acaena anserinifolia* (J.R. et G. Forst.) Druce | 7 | 0 |
| *A. novaezealandiae* Kirk | 7 | 10 |
| **Anagallis arvensis* L. | 7 | 0 |
| **Cirsium vulgare* (Savi) Ten. | 14 | 10 |
| **Digitalis purpurea* L. | 10 | 0 |
| **Galium aparine* L. | 14 | 10 |
| **Geranium molle* L. | 0 | 10 |
| *Hydrocotyle moschata* Forst. f. | 14 | 10 |
| **Hypochoeris radicata* L. | 64 | 20 |

Table 1: *Continued*

| | Younger (n=11) | Older (n=13) |
|---|---|---|
| ***Dicotyledonous herbs continued*** | | |
| **Lotus pedunculatus* Cav. | 21 | 0 |
| **Melilotus indicus* (L.) All. | 14 | 0 |
| **Mycelis muralis* (L.) Dumort. | 14 | 0 |
| **Plantago lanceolata* L. | 14 | 0 |
| **Prunella vulgaris* L. | 7 | 10 |
| **Rumex acetosella* L. | 36 | 0 |
| **Senecio jacobaea* L. | 0 | 10 |
| *Stellaria decipiens* Hook. f. | 7 | 10 |
| **Trifolium repens* L. | 14 | 10 |
| **T. subterraneum* L. | 14 | 0 |
| **Verbascum thapsus* L. | 21 | 0 |
| **Grasses** | | |
| **Agrostis capillaris* L. | 36 | 0 |
| **Anthoxanthum odoratum* L. | 21 | 0 |
| **Briza minor* L. | 14 | 0 |
| **Cortaderia selloana* (Schult.) Aesc. et Graeb. | 7 | 0 |
| **Dactylis glomerata* L. | 21 | 10 |
| **Holcus lanatus* L. | 29 | 0 |
| *Microlaena stipoides* (Lab.) R.Br. | 43 | 90 |
| *Oplismenus imbecillis* (R.Br.) Roem. et Schult. | 7 | 20 |
| **Paspalum dilatatum* Poir. | 29 | 0 |
| **Poa pratensis* L. | 7 | 0 |
| *Rytidosperma gracile* (Hook. f.) Connor et Edgar | 21 | 0 |
| **Sporobolus africanus* (Poir.) Robyns & Tourn. | 36 | 0 |
| **Other monocotyledonous herbs** | | |
| **Carex ovalis* Gooden. | 14 | 0 |
| **Juncus gregiflorus* L.A.S. Johnson | 7 | 0 |
| *Thelymitra* sp. | 7 | 0 |
| *Uncinia* spp. (mostly *U. uncinata* (Linn. f.) Kuek.) | 50 | 60 |

***Height* vs *age***

The relationship between height and age is described by the exponential function

$$\text{Height} = 34.4(1\text{-}0.993^{\text{Age}}),\ r^2 = 0.89$$

Mean annual height growth rate over all plots, indicated by linear regression ($r^2 = 0.89$, $P<0.01$, n = 24), was 21.5 cm $yr^{-1}$.

***Basal area* vs *age***

Neither teatree basal area nor total basal area showed a clear relationship with age, reflecting in part plot sizes (mean area = 50 $m^2$) which were constrained by the sizes of landslide scars and probably too small for accurate measurement of this parameter. The average total basal area in older (>37 yr) stands was 53.6 $m^2ha^{-1}$, *cf* 16.6 $m^2ha^{-1}$ in younger (<37 yr) stands; average teatree basal area in older (>37 yr) stands was 46.8 $m^2ha^{-1}$, *cf.* 15.3 $m^2ha^{-1}$ in younger (<37 yr) stands.

***Density* vs *age***

The weak relationship between teatree density and age is described by the inverse square chronofunction

$$\text{Density} = 671234\ \text{Age}^{-2},\ r^2 = 0.16$$

a poor fit because of two outliers. Teatree densities decline from tens of thousands of stems $ha^{-1}$ in stands less than 10 years old to several hundred per hectare in stands over 50 years old.

***Ground cover* vs *age***

Two broad relationships between species frequency and age were evident (Table 1). The first group of species - more common on younger (< 37 yrs) scars - are mostly introduced pasture grasses such as ratstail (*Sporobolus africanus* (Poir.) Robyns et Tourn.) and browntop (*Agrostis capillaris* L.) and herbs such as catsear and sheep's sorrel (*Rumex acetosella* L.). The second group - more common on

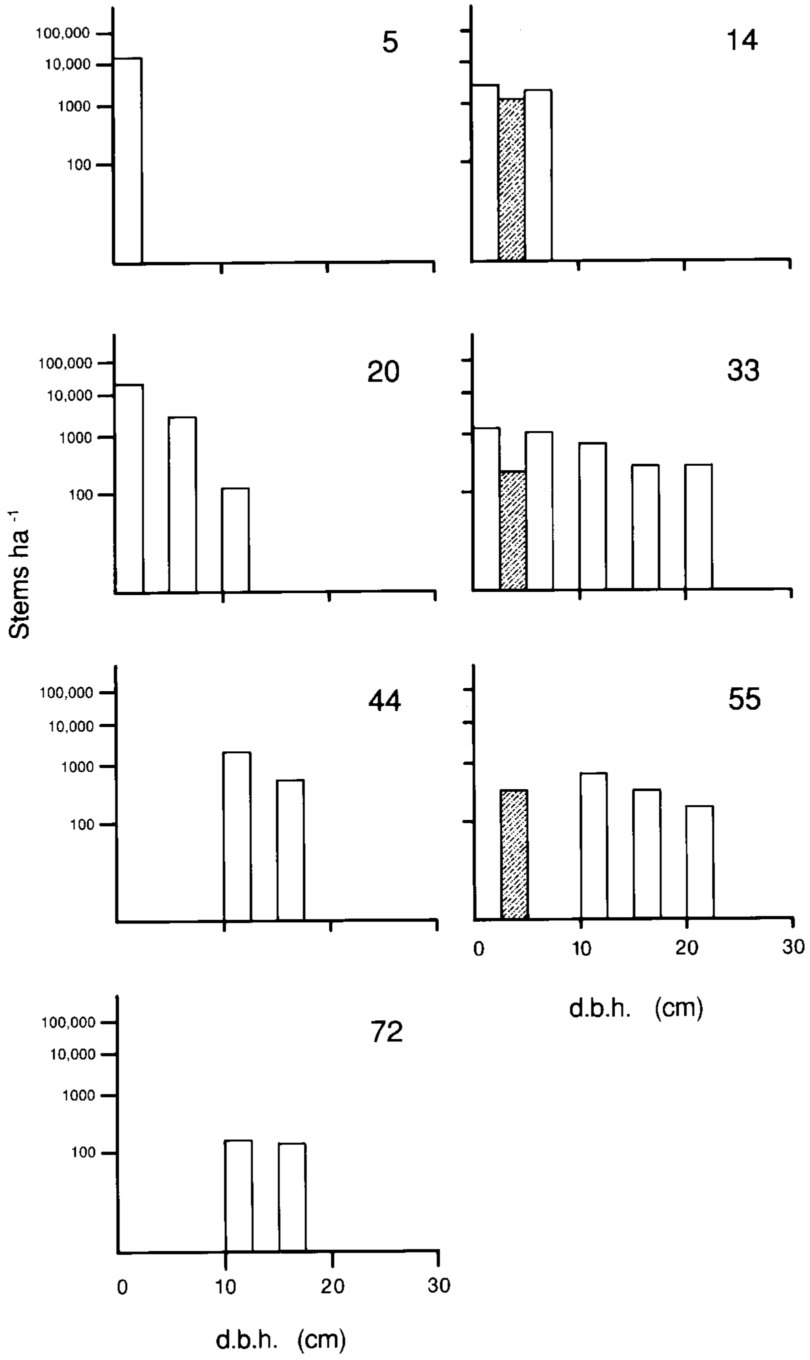


Figure 2: *Diameter distribution in seven teatree stands of various ages on landslide scars in East Cape region. Stand age in years. Hatched bars represent dead individuals.*

older (>37 yrs) scars - comprises mainly subcanopy and understorey ferns, such as common maidenhair (*Adiantum cunninghamii* Hook.) and common shieldfern (*Polystichum richardii* (Hook.) J. Smith), as well as meadow rice grass. Twiggy coprosma was present in all but the youngest stands.

Classification revealed four distinct ground layer communities. Although there was some overlap between the ages of the associated kanuka stands, mean ages differed significantly between them (p<0.01). The first community (5 plots, mean age = 11 years) was dominated by bare soil with several adventive grasses and herbs - ratstail, browntop, sheep's sorrel, paspalum (*Paspalum dilatatum* Poir.), danthonia (*Rytidosperma gracile* (Hook. f.) Connor et Edgar), and woolly mullein (*Verbascum thapsus* L.) - consistently present. Bare soil also dominated the second community (7 plots, mean age = 19 years); mosses and catsear were the only species consistently present. The third community (8 plots, mean age = 38 years) was also dominated by bare soil, but hook-sedges, meadow rice grass, common maidenhair, common shieldfern, and catsear were all widespread. Meadow rice grass dominated the fourth community (4 plots, mean age = 58 years); bare soil contributed less cover, on average, than in younger communities (44% cf. 63%), while hook- sedges, *Oplismenus imbecillis* (R.Br.) Roem. et Schult., common shieldfern, and mosses were also consistently present.

The first axis of the plot ordination (eigenvalue = 0.59) was significantly positively correlated ($r^2$ = 0.35, $P$<0.01, n = 24) with age. The species ordination followed a similar pattern with adventive grasses and herbs of the initial open stage having the lowest, and native sedges, grasses and herbs of mature teatree forest the highest scores on the first axis.

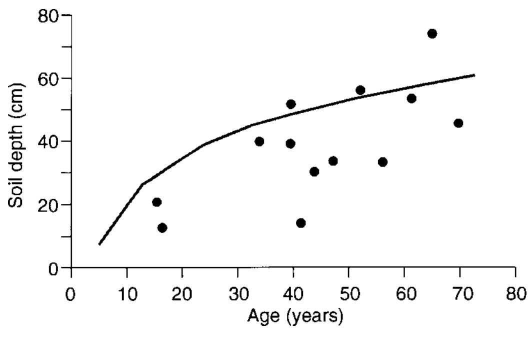


Figure 3: *Mean soil depth vs age of landslide scars in East Cape region.*

**Soil development**

Mean soil depth increased with age from an average of 20 cm at age 10 yr to 58 cm at age 70 yr (Fig. 3). The relationship between mean soil depth on landslides and age is described by the logarithmic function

$$\text{Soil depth} = 44.9 \, \text{Log}_{10} (\text{Age}) - 24.6, \; r^2 = 0.91$$

# Discussion

**Vegetation development**

Amongst the native species present in teatree stands on landslide scars, almost all the trees and many of the shrubs are early successional species characteristic of early stages of primary and secondary successions elsewhere in New Zealand. Almost all the ferns typically occur on open sites (Brownsey and Smith-Dodsworth, 1989), along with almost all the adventive grasses and herbs (Webb, Sykes, and Garnock-Jones, 1988).

Diameter and height growth rates of kanuka in primary successions on landslide scars are similar to those in stands on reverting pasture on intact regolith in the region: 0.31 cm annum$^{-1}$ *cf.* 0.26 cm annum$^{-1}$, and 21.5 cm annum$^{-1}$ *cf.* 19 cm annum$^{-1}$ respectively (Bergin *et al.*, 1995), a reflection of the inherently high fertility of the parent material. Diameter growth rates are also similar to those in primary successions on coastal sand dunes (Smale, 1994), but height growth rates are considerably faster, the latter reflecting the exposed nature of coastal dunes. A xeromorphic species (Johnson, 1984), kanuka is well adapted to cope with the poor moisture-holding capacity of juvenile soils. Although basal area - a direct indicator of biomass accumulation - could not be measured accurately in this study, the average value in older (>37 yr) stands, 54 m$^2$ ha$^{-1}$, is higher than on intact regolith in the region, 40 m$^2$ ha$^{-1}$, in stands >20 yr old (Bergin *et al.,* 1995), suggesting that the productivity of these sites, at least for the woody species present, is at least as high as that on intact regolith.

Even-aged kanuka stands in primary successions here develop along similar lines to those in secondary successions in the region (Bergin *et al.*, 1995) and elsewhere in eastern New Zealand (e.g., Allen *et al.*, 1992; Smale, 1993), sharing rapid early height growth, rapid early self-thinning, and probably rapid early increases in basal area as well. The virtually linear nature of the diameter *vs* age relationship and near-linear nature of the height *vs* age relationship - both commonly sigmoidal over the life of a tree - through the first 70 years suggests that the normally attainable lifespan of kanuka on landslide scars in the region is likely to be within the usual range of 80-150 years (Burrows, 1973).

Manuka is present in only two localities. Its prominence in the Turanganui River catchment is attributable to relatively infertile soils derived from old marine gravels; manuka is more tolerant of infertile soils than kanuka (Burrows, 1973). On Mt Whareopaia in the Tolaga Bay catchment, however, there seems to be no clear reason for its occurrence. The lower ultimate stature and shorter normal lifespan (20-40 yr: Burrows, 1973) of manuka along with its lower tolerance of shade and root competition (Burrell 1965) ensure that where both species grow together, manuka is usually eliminated over the first 20 or so years (Esler and Astridge, 1974); manuka is more-or-less absent from secondary stands >30 years old in the region (Bergin *et al*., 1995). Manuka was still present in stands up to 50 years old on Mt Whareopaia, although subdominant to kanuka, usually with much smaller diameters and in the oldest stand, mostly dead; in the Dunedin district manuka occurred in stands up to 50 years old (Allen *et al*.,1992).

Several stages in primary successions on landslide scars in extensively-grazed pastoral landscapes in the East Cape region can be distinguished, in which development of the ground layer largely reflects the dynamics, dominated by intraspecific competition, of the even-aged teatree stands growing on them. Initially, bare substrate dominates, with scattered teatree seedlings, grasses such as ratstail and browntop, and herbs such as sheep's sorrel and woolly mullein typical of the surrounding pasture. By about 15 years, dense self-thinning thickets of teatree with some twiggy coprosma have developed; the adventive grasses and herbs in the ground layer of the earlier open stage are progressively excluded by the deep shade cast by the overstorey. By about 30 years, short closed-canopy forest is evident, with a subcanopy of mingimingi (*Leucopogon fasciculatus* A. Rich.) locally present and a ubiquitous understorey of twiggy coprosma. Thinning of the teatree canopy is largely complete, allowing light levels sufficient for hook-sedges, meadow rice grass, common maidenhair, and common shieldfern to begin establishing in a ground layer from which pasture grasses and herbs have all but vanished.

Over the next four decades at least, fewer changes are evident, with barely perceptible increases in canopy height and decreases in density, disappearance of mingimingi through natural senescence (maximum lifespan approx. 30 yr: Bray, 1989), and persistence of twiggy coprosma. From about 50 years, plants - including occasional seedlings of other canopy tree species - cover most of the ground, meadow rice grass being dominant. The increase in meadow rice grass from about 30 years may reflect an increasingly acidic litter layer; in *Pinus radiata* plantations in the central North Island this grass characterises sites low in exchangeable cations (Allen, Platt, and Coker, 1995). In spite of their occurrence in landscapes dominated by introduced plants, adventive species are prominent only in the initial open stage of primary successions on landslide scars and - notwithstanding the presence of catsear in stands <50 years old - are subsequently insignificant. Secondary kanuka stands in the Dunedin district share the exclusion of pasture species by shading from 13 years, suppression of most other species until 50 years, and rarity of seedlings of other canopy species until at least 70 years (Allen *et al*., 1992).

Before its wholesale destruction for agriculture late last century and early this century, primary forest dominated by tawa (*Beilschmiedia tawa* (A. Cunn.) Kirk) and kohekohe (*Dysoxylum spectabile* (Forst. f.) Hook. f.) covered most of the study area (Leathwick *et al.,* 1995). Both highly shade-tolerant species (Smale and Kimberley, 1983), neither was present in the plots, though they are still widespread in remnants of primary forest in the region (Leathwick *et al*., 1995). Only one characteristic subcanopy species of primary forest occurred, and only very locally - mahoe (*Melicytus ramiflorus* ssp. *ramiflorus* Forst. et Forst. f.), also a widespread successor of kanuka in seral forest (*e.g.,* Baylis, 1967; Smale, Hall, and Gardner, 1995). Earlier successional species like mapau (*Myrsine australis* (A. Rich.) Allan) were also very local, even in older stands. In ungrazed stands the relative abundance of such species in secondary teatree adjacent to primary forest - for example, upper Thumb Ridge, Little Barrier Island (Smale, 1993) and their scarcity in other stands distant from primary forest - *e.g*., Thornton, Bay of Plenty (Smale, 1994), Dunedin district (Allen *et al.,* 1992) - suggests that the occurrence of potential successors in seral kanuka forest is correlated with distance from seed sources of these species. None of the stands studied is more than 2 km from remnants of primary forest, and so all are within range of seed sources of later successional species such as tawa and kohekohe. New Zealand pigeon or kereru - *Hemiphaga novaeseelandiae* (Gmelin), the only surviving disperser of these species (Clout and Hay, 1989), are still widespread in the region (Bull, Gaze, and Robertson 1985) although intensively studied populations elsewhere in the country are all declining (Clout, Karl, Pierce, and Robertson, 1995).

All stands studied here are grazed to some extent and many of these potential successors are highly palatable to domestic stock (Beveridge, 1977). Kanuka forest elsewhere in the country subject to moderate browsing pressure from feral red deer (*Cervus elaphus* L.) or fallow deer (*Dama dama* (L.)) exhibits 'stalled' or partially stalled successions, with further cohorts of kanuka establishing in the scarcity or absence of more palatable broadleaved species (Payton, Allen, and Knowlton, 1984; Smale *et al*., 1995). Abundant twiggy coprosma and a near absence of large-leaved species such as mahoe and hangehange (*Geniostoma rupestre* Forst. et Forst. f.) characterise secondary teatree stands in the Waitakere Range subject to cattle (*Bos taurus* L.) grazing (Esler and Astridge 1974), features shared with these stands. Despite the proximity of them to seed sources of many later successional trees in primary forest remnants, continued grazing will stall their transition to tall forest, and further cohorts of kanuka are likely on at least some sites. Even if grazing were to cease, dense understories of twiggy coprosma might - for a while - inhibit the development of such cohorts and of other tree species as well (Baylis, 1967).

Primary successions on landslide scars in lowland Taranaki on somewhat similar lithology but under twice the annual rainfall follow markedly different pathways from those in the East Cape region, being characterised by open herbaceous vegetation at 5 years, tree fern (*Dicksonia squarrosa* (Forst. f.) Swartz-*Cyathea smithii* Hook f.) scrub at 25 years and short forest dominated by kamahi (*Weinmannia racemosa* Linn. f.) at 50 years (Blaschke *et al*., 1992). Tawa, the old-growth canopy dominant of the region, does not become prominent until 150 years after initiation. The predominance of tree ferns and kamahi in the Taranaki pathway, in contrast to kanuka here, is likely to result from the wetter climate there. *D. squarrosa* and *C. smithii* are typical species of wetter climates (Brownsey and Smith-Dodsworth, 1989) and kamahi is a relatively drought-intolerant species (Wardle, 1966); only relatively drought-tolerant *Cyathea dealbata* (Forst. f.) Swartz is at all common in the study areas and kamahi is virtually absent.

The establishment on landslide scars of the initial woody dominant - kanuka - within a few years of new surfaces becoming available is shared by other primary successions in New Zealand involving teatree, *e.g.,* on sand dunes (Smale, 1994) and alluvial terraces (Dobson, 1979), as well as primary successions involving other species, *e.g.,* southern rata (*Metrosideros umbellata* Cav.) and kamahi on glacial moraines and on shattered bedrock on landslide scars in western South Island (Wardle, 1991).

**Soil development**

Observation suggests that soil development on landslides here is consistent with that outlined by Trustrum and de Rose (1988); *i.e*., initial rafted material followed by collapse of the headwall enhanced by animal movement, giving greatest soil depth marginal to the head and sidewall and slower soil formation elsewhere due to weathering of the bedrock. Because of the intact vegetation on the landslides consistent identification of rafted material was not always possible, especially on older landslides.

Soil development rates on landslides here are substantially faster than those studied by Trustrum and de Rose (1988). Although slope angle was slightly greater on average in the inland Taranaki study (34$^o$, as against 30$^o$) and annual rainfall was somewhat higher (1840 mm, *cf.* 1200 - 1600 mm), the greatest contribution to the contrast in the rate of soil formation is likely to result from differences in parent rock. On sandstone in Taranaki, Trustrum and de Rose (1988) observed platy structured rinds flaking off the bedrock whereas mudstone bedrock at our study sites, if not already frittered, tends to fritter rapidly into 1-2 cm blocks upon exposure. With wetting and drying these blocks reduce in size relatively quickly to become gravels in a silty clay matrix (McLeod, Rijkse, and Dymond, 1995). Informal observations during field work also suggest that the loose, pedal nature of the intact mudstone soil profile of the headwall results in faster headward erosion by collapse than on similar profiles in nearby sandstone, where the soil is not so strongly pedal. Further work is needed to confirm this hypothesis.

# Acknowledgements

This study was funded by the Crown through the Foundation for Research, Science and Technology under Contract C09232. Dr M. Marden and D. Rowan (Landcare Research, Gisborne) freely shared their knowledge of the district with us. The Gisborne office of the Department of Survey and Land Information allowed use of aerial photographs of the region. G.F. Pardy, P.T. Whaley, and M.A. McLeod provided field assistance, and station owners gave permission to work on their properties. D.K. Emmett and Dr B.R. Burns assisted with data analysis, and Pauline Hunt and P.G. Neville produced the figures. C.T. Duval and Drs B.R. Burns, B.D. Clarkson, and M. Marden, and two anonymous referees made helpful comments on earlier drafts.

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