

An Experimental Study of Regeneration on Landslides in Montane Rain Forest in Jamaica



J. W. Dalling; E. V. J. Tanner

The Journal of Ecology, Vol. 83, No. 1 (Feb., 1995), 55-64.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28199502%2983%3A1%3C55%3AAESORO%3E2.0.CO%3B2-C>

The Journal of Ecology is currently published by British Ecological Society.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact jstor-info@umich.edu.

An experimental study of regeneration on landslides in montane rain forest in Jamaica

J. W. DALLING* and E. V. J. TANNER

Department of Plant Sciences, University of Cambridge, Downing St. Cambridge CB2 3EA, UK

Summary

1 Tree seedlings of *Alchornea latifolia* (Euphorbiaceae), *Clethra occidentalis* (Clethraceae), and *Vaccinium meridionale* (Ericaceae), were transplanted into five recent 'debris flow' landslides, and five adjacent understorey areas, in montane forest between 1450 m and 1770 m in the Blue Mountains, Jamaica. Organic fertilizer and protective barriers were applied in a 2 × 2 factorial design.

2 Mortality (all species) in the 15 months following transplanting was 30% on landslides, and 46% in the understorey. Mortality was significantly higher in the understorey than on landslides for *Alchornea* and *Vaccinium*, but was not different for *Clethra*. In the understorey there was a peak of mortality for *Alchornea* and *Vaccinium* in the dry season, but no associated peak on landslides. There was no effect of fertilizer or barrier treatment on seedling survival.

3 Height growth of unfertilized *Clethra* and *Vaccinium* (but not *Alchornea*) seedlings was greater on landslides than in the understorey. On landslides fertilization increased biomass (but had no effect on height) for all species. There were no significant effects of fertilizer in the understorey.

4 Soil nutrient concentrations were much higher in understorey soils than landslide soils, pH values were similar.

5 Foliar nitrogen concentrations for transplanted seedlings were lower on landslides than in the understorey, while foliar phosphorus concentrations were not different. Fertilization did not change foliar nitrogen concentrations on either landslides or the understoreys, whereas there was a significant increase in phosphorus concentration in fertilized seedlings on landslides.

6 Soil water content varied less on landslides than in understoreys; soils from three of the landslides were judged to be near field capacity throughout the year. In the understoreys there were significant shortages of water in the dry season which correlated with increased mortality in the transplanted seedlings.

7 Thus we have shown that growth of seedlings on landslides is limited by nutrient supply; water supply and soil movement do not limit growth of established seedlings. In the understoreys seedling growth is limited by photosynthetically active radiation, nutrient supplies may limit seedling growth due to root competition, and seasonal drought is correlated with increased mortality.

Keywords: *Alchornea latifolia*, barrier, Blue Mountains, *Clethra occidentalis*, fertilizer, nutrients, seedling, soil moisture, tropical, understorey, *Vaccinium meridionale*

Journal of Ecology (1995) **83**, 55–64

Introduction

In forests characterized by steep slopes, landslides may be an important component of the disturbance

*Present address: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, Miami, Florida, USA.

Correspondence: E. V. J. Tanner.

regime. At different spatial scales, landslides have been reported to be important for the regeneration of particular species, or guilds of species (Whitmore 1975; Herwitz 1981; Guariguata 1990), and in determining overall forest structure (Veblen & Ashton 1978; Veblen 1979; Stewart 1986).

Landslides differ from treefall gaps in several ways.

These include a scarcity or complete absence of advance regeneration, together with an impoverished soil seed bank (Garwood 1985; Guariguata 1990), a low soil nutrient status (Flaccus 1959; Adams & Sidle 1987; Guariguata 1990), an unstable substrate (Nakamura 1984), and possibly a lack of a mycorrhizal inoculum (J. Lodge, personal communication). In common with treefall gaps, landslides have higher photosynthetically active radiation (PAR) levels, and probably different soil water relations than the forest understorey.

In montane forest in Jamaica, colonization of landslides appears to be very slow. Pioneer species characteristic of disturbed areas along the forest margin, and large treefall gaps, such as *Trema floridanum* and *Brunellia comocladifolia* are infrequent on landslides, as are herbaceous species and ferns. The earliest landslide colonizers appear to be primarily ericoid woody species, followed by the nitrogen-fixing lichen *Stereocaulon virgatum* (Dalling 1994). In this study a subset of the factors which could control regeneration on landslides were investigated using seedlings of native tree species transplanted onto recent landslides, and for comparison, into the understorey of adjacent intact forest. The specific questions addressed were: (i) are there differences in the mortality and growth of seedlings on landslides and in the forest understorey, and do these differences reflect the observed ability of these species to colonize landslides? (ii) Is nutrient availability the factor of paramount importance determining growth on landslides, and does nutrient availability limit seedling growth in the forest understorey? (iii) Do rockfalls or substrate movement have an effect on seedling mortality and growth on landslides? (iv) Does the availability of soil water control seedling survival and growth on landslides?

Materials and methods

The study area is in the western Blue Mountains (18°05'N; 76°39'W) between 1460 and 1770 m a.s.l. (Fig. 1). Annual rainfall averages 2500–3000 mm with a dry season from June to August; mean monthly maximum and minimum temperatures are *c.* 20 °C and 11 °C (Kapos & Tanner 1985). The five landslides investigated in this study are near to the crest of the main ridge of the Blue Mountains, in 'Wet Slope Forest' (*sensu* Grubb & Tanner 1976; Fig. 1, Table 1), except landslide four which is about 2 km south of the main ridge in secondary forest. Plant names follow Adams (1972).

The landslides investigated were all triggered in September 1988 by Hurricane Gilbert. All the landslides were 'debris flow' type (*sensu* Varnes 1958), characterized by a liquefaction of the topsoil and root-zone during the triggering event, leaving a relatively smooth eroded surface almost entirely devoid of vegetation. In all cases the remaining coarse-grained material was largely composed of Richmond deposit

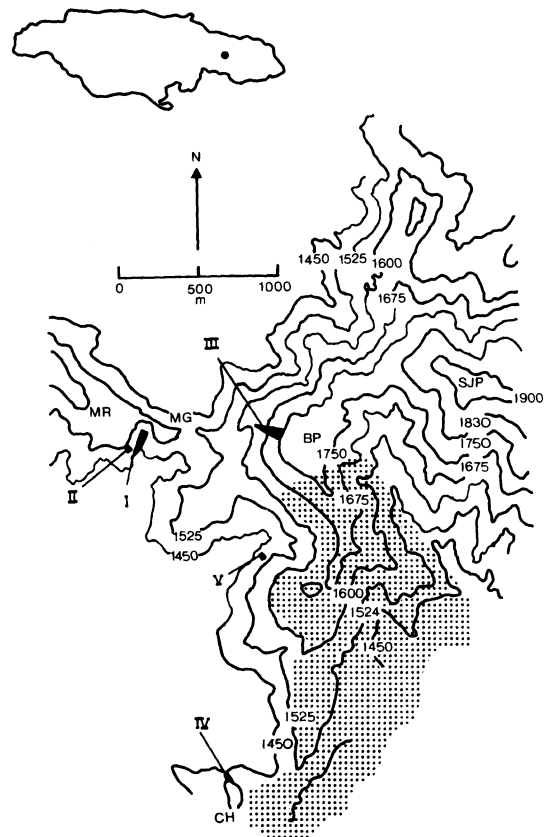


Fig. 1 Location of field sites (landslides I–V) in the Blue Mountains. Mapped area extends only above the 1450 m contour. Contour interval = 75 m. Stippling indicates area cleared of forest. MR = Mull Ridge; MG = Morce's Gap; BP = Bellvue Peak; SJP = Sir John's Peak; CH = Cinchona Hill.

sandstone. With the exception of landslide II, landslides lacked 'deposition zones', as eroded material was washed away by pre-existing streams. Consequently all seedlings were transplanted into the 'erosion zone' of the landslide; this zone corresponds to the 'upper zone' (Guariguata 1990), or 'scar zone' (e.g. Shimokawa 1984) in other studies.

THE SPECIES TRANSPLANTED

Three native tree species, *Alchornea latifolia* Euphorbiaceae, *Clethra occidentalis* Clethraceae, and *Vaccinium meridionale* Ericaceae, were used in the transplant experiment. *Alchornea* seedlings were abundant in the understorey, having germinated in response to increased light caused by Hurricane Gilbert, and were collected locally at each site. *Clethra* and *Vaccinium* were collected from an abandoned road cutting close to landslide III (Fig. 1). At the time of transplanting, seedlings of all species ranged between three and seven centimetres in height. Seedlings of *Alchornea* were all < 6 months old at the time of transplanting, *Clethra* and *Vaccinium* seedlings could not be aged but may have been several years old; these age differences may have affected the response of the species to the treat-

Table 1 The locations and sizes of the landslides

Landslide	Aspect	Slope (°)	Altitude (m a.s.l.)	Width (m)	Length (m)	Area (ha)
I	150°SE	52	1525	10	50	0.05
II	130°SE	50	1525	6	10	0.006
III	290°NW	35	1770	19	200	0.38
IV	000°N	55	1460	7	19	0.01
V	270°W	45	1425	8	12	0.009

ments; in particular the older seedlings may have been less responsive.

Alchornea is a gap-demanding species, and one of the commonest and fastest-growing species in the forest. In artificially created gaps it showed the greatest increase in maximum seedling height of all species (Healey 1990). *Alchornea* was the only species transplanted not seen regenerating on landslides though it has been reported growing on the comparatively nutrient-rich deposition zones of recent landslides in lower montane forest in Puerto Rico (Guariguata 1990).

Clethra is the principal canopy species in the forest as a whole (Tanner 1977) and is also gap-demanding, showing an overall decrease in density during a 10-year period without disturbance (Healey 1990), and significantly more recruitment following artificial gap creation than in undisturbed plots (Sugden *et al.* 1985; Healey 1990). The regeneration of the small seeded *Clethra* may be as much determined by substrate as by the light environment, as its predominant distribution as a seedling is on nurse logs or tree-fern stems, and along road cuttings and embankments; it is virtually absent from the forest floor where there is a continuous litter layer (Newton & Healey 1989). The distribution of *Clethra* in gaps might therefore partly be explained by the creation of new microsites with substrates favourable for establishment, as well as increased light (Healey 1990).

The regeneration requirements of *Vaccinium* are less well known. From general observations it seems that *Vaccinium* requires a combination of large gaps and exposed mineral soil for seedling establishment. *Vaccinium* seedlings are seldom seen in the forest understorey, and have only rarely established in the root pits created by tree-falls following Hurricane Gilbert (P. Bellingham personal communication). However, in large gaps, and at the forest margin where there has been some soil disturbance, seedlings do establish (Sugden *et al.* 1985). Once established, persistence of *Vaccinium* in the canopy appears to be through basal sprouts.

EXPERIMENTAL DESIGN

Within each of the five landslides, and in five adjacent understorey sites, two blocks separated by 5 m were

set up, each containing four 1-m² plots. Each 1-m² plot was randomly assigned to one of four treatments, and within each 1-m² plot, 10 seedlings of each species were planted in 0.25-m² subplots. Blocks were positioned so as to ensure that the substrate was as comparable as possible (e.g. 'rafts' of organic material remaining on the landslide surface, and drainage rills were avoided). The understorey areas were located in nearby forest with similar slope and aspect to the landslides. Plots in the understorey areas were placed in positions equivalent to the plots on the landslides. Landslide II, but not its corresponding understorey area, was subsequently removed from the data analysis, as continued slumping of soil at this site killed almost all transplanted seedlings, and created a depositional zone over one block.

The four 1-m² plots per block were randomly assigned each to a different treatment (control, barrier, fertilizer, fertilizer + barrier) to give two main effects in a factorial analysis. The barriers consisted of sheets of galvanized steel 1 m long by 0.3 m high, positioned 10 cm up-slope of each barrier treatment plot. Fertilized seedlings received 15 ± 0.5 g of commercial organic fertilizer (1.70% N, 1.98% P, 2.28% K, 0.75% Mg, 5.28% Ca; our analysis) in each seedling hole before the seedling was planted. Organic, rather than inorganic, fertilizer was used to limit leaching losses and contamination of unfertilized plots.

SEEDLING TRANSPLANTATION, GROWTH MEASUREMENT AND HARVEST

Seedlings, with c. 200 cm³ of soil intact around the roots, were transplanted between April and August 1989; the order in which sites, and plots within sites were transplanted was randomized. Seedlings transplanted during the dry season (June–August 1989), were watered for a week following transplanting, and were shaded for the first 3 weeks to promote establishment. Seedling heights were measured at transplanting, and in September 1989, January, May, August and November 1990 (exact dates in Dalling 1992). In February 1991 median and maximum-sized seedlings of each species were dug up from one (randomly chosen) block of the two at each site, and total above-ground dry mass and leaf area measured.

Maximum-sized seedlings were chosen as the most likely of the seedlings to persist in the long term. Median-sized seedlings however, are more typical of the growth performance of the seedlings in the plot; they are more appropriate than the mean, which can be skewed by large numbers of small, suppressed seedlings.

Statistical analysis of total mortality data was made using the Yates-corrected G -statistic (G_c ; Zar 1984). Subsequently, arcsine-transformed percentage mortality for each census interval was compared by ANOVA. Pre-September 1989 data were excluded to remove the effects of transplant shock.

Statistical analyses of height data from November 1990, and harvested dry mass, and leaf area data were analysed by ANOVA.

SOIL CHEMISTRY

Soil chemical analyses were conducted using methodologies outlined by Anderson & Ingram (1989). Nitrogen mineralization and pH were measured in fresh soils in Jamaica; the other analyses were done on dry soils in Britain. Nitrogen mineralization was measured between January and February 1991. Three pairs of intact 5 cm diameter and 10 cm deep cores were taken per landslide (and the same per understorey area). One of each pair was removed immediately, kept cool, and a homogeneous sub-sample excluding rock fragments of > 0.5 cm extracted in 2 M KCl (1:5 soil to solution ratio) within 18 h. The other core was left to mineralize *in situ* for three weeks and then extracted. Ammonium and nitrate concentrations in extracts were assayed colorimetrically.

Bicarbonate (0.5 M, pH 8.5) extractable phosphate and exchangeable bases were measured in composite 0–10-cm samples, one sample for each of the landslides and each of the understorey areas. Exchangeable bases were extracted by leaching soil samples with successive aliquots of ammonium acetate at pH 7, over a period of 3 h. Potassium was measured by flame emission, and calcium and magnesium by atomic absorption, using a background of lanthanum chloride. Loss-on-ignition (450 °C, 12 h) was measured on one pooled sample (from 10 subsamples) per site using one monthly collection of cores 2 cm in diameter by 10 cm deep (see soil water below).

FOLIAR NUTRIENTS

Leaves of the harvested seedlings were digested in concentrated sulphuric acid with mercury as a catalyst, and hydrogen peroxide. Resulting solutions were analysed for nitrogen and phosphorus (Chemlab Instruments Methods Sheets CW2-008-11, 1982 and CW2-075-01, 1983). A sample of standard leaf material was also processed with each batch to check for accuracy, this standard material was analysed by independent laboratories which confirmed our analy-

sis. Initial analyses were on samples pooled by treatment to make eight composite samples (landslide or understorey × fertilized or not × with barrier or not). Where results from composite samples indicated a possible treatment effect analyses were repeated using separate samples from each of the sites.

SOIL WATER

Soil water content (% dry mass) was measured at the end of each month by taking 10 soil cores, 2 cm in diameter, from a depth of 0–10 cm at random locations around the seedling plots at each of the landslide and understorey sites. Monthly soil water content data were analysed by repeated measures ANOVA. Soil moisture characteristic curves were derived from pooled fresh samples, one for landslides and one for understorey areas (equal amounts of soil from each of the landslide and understorey sites) using a pressure plate apparatus (Soil Moisture Equipment Company, Santa Barbara, California). In addition to the measurement at field capacity (0.03 MPa) made with the pressure plate apparatus, field capacity and bulk density of two samples of soil from each of the landslide and understorey sites were measured in Jamaica using intact soil cores (5 cm in diameter, 10 cm depth). Cores were saturated for 24 h, allowed to drain for 48 h and then weighed.

Rainfall was measured weekly with a five-inch rain gauge at 1550 m on the main ridge crest of the Blue Mountains. This is probably representative of sites I, II, III, V, but may over-estimate of the rainfall at site IV, which is further South, in the rain-shadow of the main ridge.

Results

MORTALITY

Mortality for all species over the 15-month period was 30% of seedlings transplanted onto landslides, and 46% of seedlings transplanted into the understoreys (Fig. 2). Mortality was significantly higher in the understoreys than on landslides for *Alchornea* ($G_c = 56.9$, $P < 0.001$) and *Vaccinium* ($G_c = 89.0$, $P < 0.001$), but was similar in both environments for *Clethra* ($G_c = 3.1$, NS). Mortality of *Alchornea* was always greater than *Clethra*; mortality of *Vaccinium* was extremely variable between sites, ranging from 7% to 80%.

In the understoreys percentage mortality peaked at the fourth census, and was significantly higher for *Alchornea* and *Vaccinium* ($F_{1,438} = 79.5$; $P < 0.001$), when contrasted with mortality in the second, third and fifth censuses. This increase in mortality rate coincided with the dry season. Finally, no significant

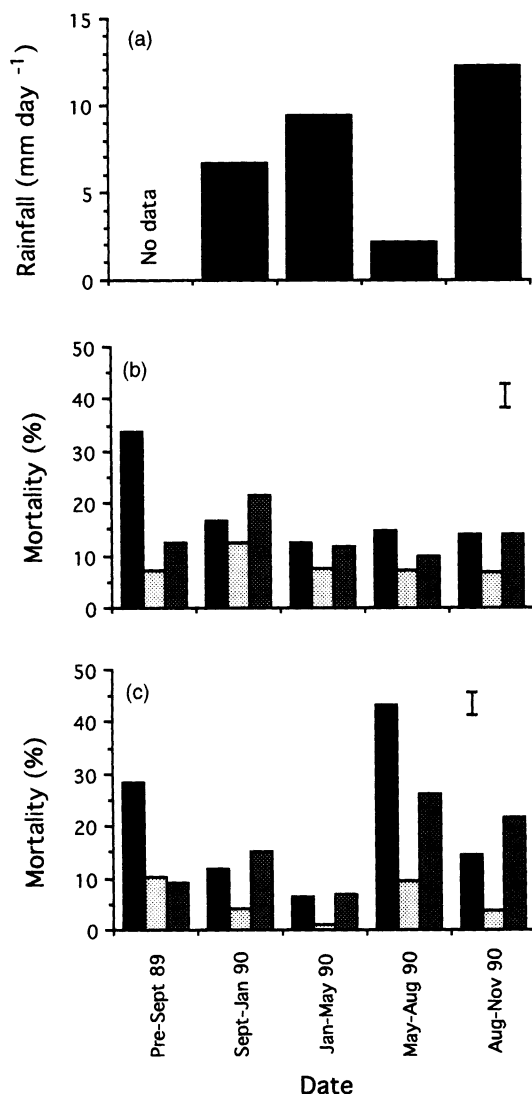


Fig. 2 (a) Rainfall for each census period in mm day^{-1} . (b) Percentage mortality on landslides and (c) percentage mortality in the understorey for *Alchornea* (■), *Clethra* (□) and *Vaccinium* (▨). Percentage mortality is the number of seedlings dying during each census interval divided by the number of seedlings alive at the beginning of the census interval ($\times 100$). Non-transformed data are shown in the figure, plotted values are means; the error bars equal one standard error of the difference of means.

effects of either fertilizer or barrier were found on mortality on landslides or in the understoreys.

SEEDLING GROWTH

Comparisons between landslides and understoreys and between species

Dry mass and leaf area were significantly higher on landslides than in the understoreys for *Clethra* and *Vaccinium*, but not for *Alchornea* (Fig. 3); maximum-sized seedlings of *Vaccinium*, and median-sized seedlings of both *Clethra* and *Vaccinium* were significantly taller on landslides than in the understoreys. *Alchornea* seedling height was not significantly different between the landslides and understoreys.

Effect of fertilizer and barriers (Fig. 3)

On landslides total dry mass was significantly greater in fertilized maximum-sized seedlings of *Alchornea* and median-sized seedlings of *Alchornea*, *Clethra* and *Vaccinium* (Fig. 3c); leaf area was significantly greater in fertilized maximum-sized seedlings of *Alchornea* and median-sized seedlings of *Clethra* (Fig. 3d). There were no significant effects of fertilizer on seedling height (Fig. 3a,b), although *Alchornea* showed a trend towards greater seedling height when fertilized for both median and maximum-sized seedlings.

There were no significant effects of barriers on biomass or seedling height (Fig. 3b); although the barriers had the intended effect of reducing soil and rock movement across the seedling plots, with a mean amount of soil accumulated behind each barrier on landslides of 4.5 kg (range 0.5–18.5 kg fresh mass between September 1989 and February 1991).

SOIL AND FOLIAR NUTRIENTS

Soil nutrient concentrations were much higher in understorey soils than landslide soils (Table 2). *In situ* incubation of intact soil cores failed to

Table 2 Mean (± 1 SEM) soil chemical analyses for landslide and understorey soils (0–10 cm depth)

	Landslides	Understoreys
KCl extractable NH_4 ($\mu\text{g g}^{-1}$)		
time 0 weeks	0.84 ± 0.02	3.87 ± 0.04
time 3 weeks	0.84 ± 0.02	3.38 ± 0.04
Bicarbonate extractable P ($\mu\text{g g}^{-1}$)	4.8 ± 2.1	21.4 ± 4.0
pH	4.6 ± 0.1	4.4 ± 0.3
Exchangeable Mg (mequiv 100 g^{-1})	2.0 ± 1.2	3.1 ± 0.7
Exchangeable Ca (mequiv 100 g^{-1})	3.3 ± 0.9	6.0 ± 1.4
Exchangeable K (mequiv 100 g^{-1})	1.1 ± 0.2	2.2 ± 0.4
Bulk density (g cm^{-3})	0.78 ± 0.06	0.37 ± 0.03
Loss-on-ignition (%)	2.6 ± 0.6	21.8 ± 5.2

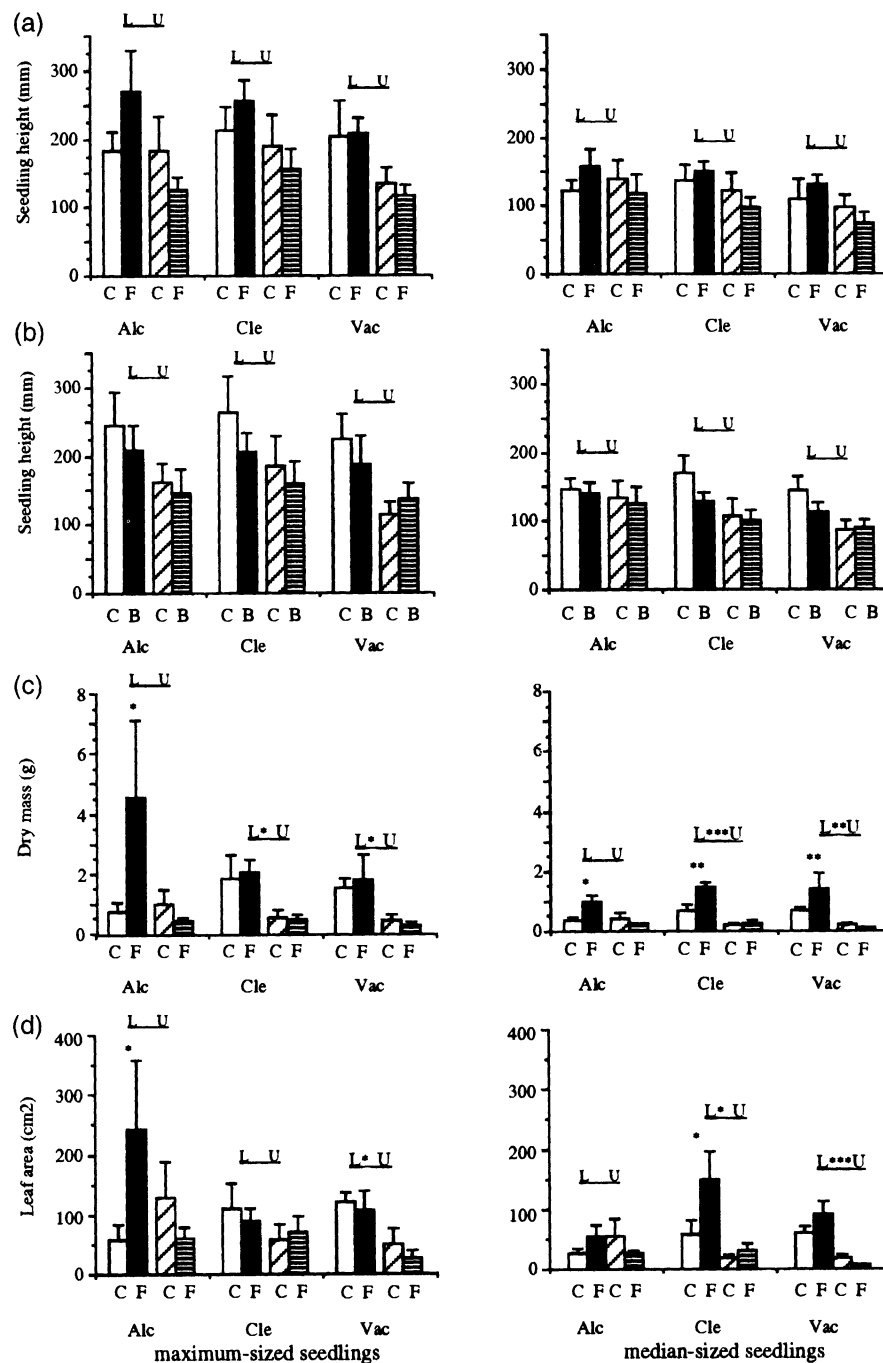


Fig. 3 (a) Seedling height in November 1990 on landslides and in the understoreys with and without fertilizer; (b) seedling height with (B) and without (C) protective barrier; (c) above-ground dry mass with and without fertilizer; (d) leaf area with and without fertilizer. Maximum-sized seedlings are shown in the left-hand column, median-sized seedlings in the right. Values are means ± 1 SEM. Significant differences between fertilized (F) and control (C) and between landslides (L) and understoreys (U) are indicated as follows * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Significant differences in seedling heights are shown in Table 3. Alc = *Alchornea*, Cle = *Clethra*, Vac = *Vaccinium*.

show any nitrogen mineralization, although pools of ammonium were four to five times larger in the understorey than on landslides. Nitrate concentrations were below the detectable limits of $0.5 \mu\text{g g}^{-1}$ using this methodology. Soil pHs were similar *c.* 4.5 on landslides and understoreys.

Leaf nitrogen concentrations were lower in seedlings from landslides than from those from the understoreys in *Alchornea* (one tail *t*-test, $n = 3$, $P < 0.05$) but not for *Clethra* or *Vaccinium*; fertilization did not change foliar nitrogen concentrations (Fig. 4a). Leaf phosphorus concentrations were similar in under-

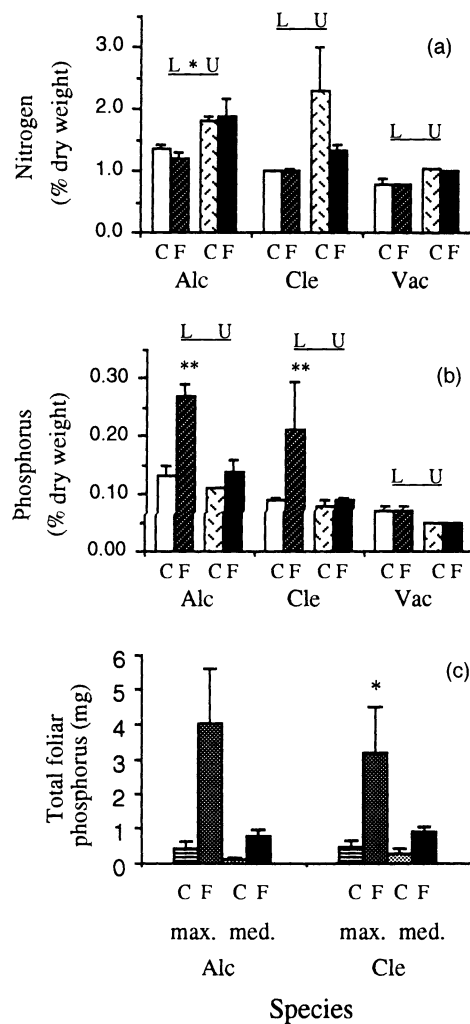


Fig. 4 (a) Percentage nitrogen concentration in leaves and (b) percentage phosphorus concentration in leaves. Means \pm SEMs for two samples: one pooled sample for median and one pooled sample for maximum-sized seedlings, except for *Vaccinium* in the understoreys where only one pooled sample was analysed. Additionally P concentrations in leaves of fertilized and unfertilized seedlings of *Alchornea* and *Clethra* were measured in nine pooled samples, one from each of the four landslides and the five understoreys, and used for the statistical comparisons shown in (b) and (c). Landslides without fertilizer (\square), with fertilizer (\blacksquare); understoreys without fertilizer (\square), with fertilizer (\blacksquare). (c) Mean (\pm 1 SEM) total foliar phosphorus from landslides for *Alchornea* and *Clethra* only ($n = 4$). NB concentrations from each site were used to calculate contents, not those in (b). (\square) Maximum-sized unfertilized seedlings; (\blacksquare) maximum fertilized seedlings; (\square) median unfertilized seedlings; (\blacksquare) median fertilized seedlings. Significant differences between fertilized (F) and control (C) are indicated as follows: * $P < 0.05$; ** $P < 0.01$.

tillized seedlings on landslides and understoreys; fertilization increased phosphorus concentrations for *Alchornea* and *Clethra* on landslides (Fig. 4b; $P < 0.01$). Total phosphorus content in maximum-sized seedlings of *Clethra* was also increased by fertilization (Fig. 4c; $P < 0.05$).

Table 3 Statistically significant differences from Fig. 3

Treatment/Comparison/Species	Maximum or median size	d.f.	F-value from ANOVA	P
landslide > understorey				
Dry mass				
Cle	max	1,7	7.21	<0.05
Cle	med	1,7	35.8	<0.001
Vac	max	1,7	8.07	<0.05
Vac	med	1,7	14.38	<0.01
Leaf area				
Cle	med	1,7	7.85	<0.05
Vac	max	1,7	8.33	<0.05
Vac	med	1,7	37.06	<0.001
Height				
Vac	max	7	t-test	<0.05
Cle	med	7	t-test	<0.05
Vac	med	7	t-test	<0.01
fert > unfert. on landslides				
Leaf area				
Alc	max	1,18	6.11	<0.05
Cle	med	1,18	5.00	<0.05
Dry mass				
Alc	med	1,18	5.32	<0.01
Cle	med	1,21	4.45	<0.05
Vac	med	1,17	6.81	<0.05

SOIL WATER

Annual rainfall for 1990 was *c.* 2700 mm (Fig. 5). Potential evapotranspiration is *c.* 800 mm year⁻¹ (Kapos & Tanner 1985), reaching 100 mm month⁻¹ in the dry season. Thus potential evapotranspiration exceeded rainfall for May, June, July and part of August. On landslides I, III and V, soil water content did not change significantly through the year; on landslides II and IV, soil water content was significantly lower in the dry season (May, June and July, $P < 0.05$; Fig. 5). Variation in soil water content in the understoreys was far greater than on landslides, with significantly lower soil moisture contents for all sites in June, July and August (Fig. 5; $P < 0.05$).

The soil moisture characteristic curves for landslide and understorey soils (Fig. 6) show that landslide soils (with low organic matter and high bulk density; Table 2) have lower water contents than understorey soils at the same water potential. Interpreting water availability for particular sites is made difficult because these curves are derived from pooled, disturbed samples. Furthermore, for landslides, field capacity and wilting point contents differ by only 10–15%.

Discussion

PATTERNS OF MORTALITY AND GROWTH

On landslides the mortality rate of transplanted seedlings was quite low for all three species, including

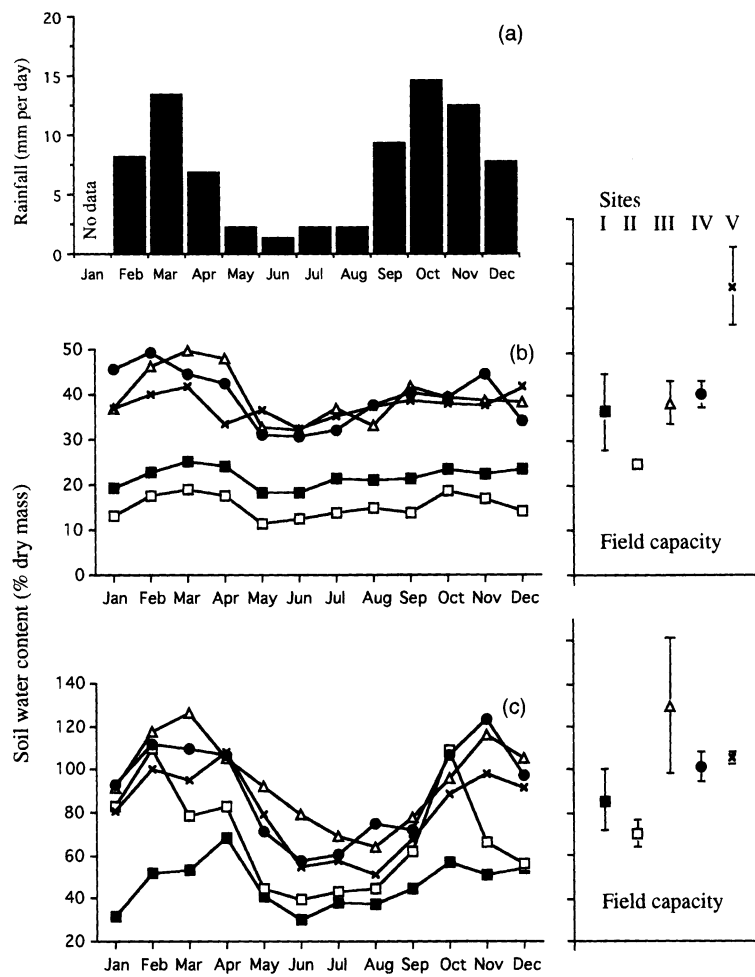


Fig. 5 (a) Monthly rainfall and soil water contents at the end of each month on (b) landslides and (c) in the understoreys in 1990 and field capacities from undisturbed soil cores for each site (mean \pm SEM, $n = 2$).

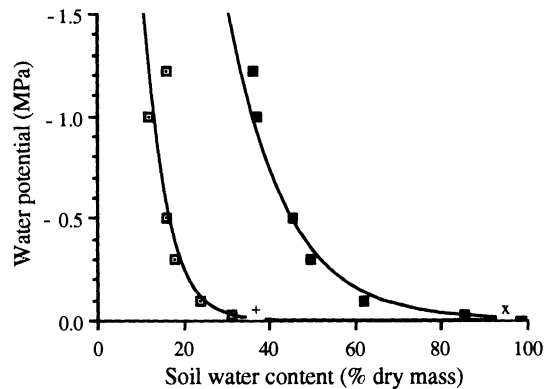


Fig. 6 Soil moisture characteristic curve of soil water content versus soil water potential using a pressure plate apparatus ($n = 5$ replicates per water potential), for landslide soils (\square), understorey soils (\blacksquare). Mean field capacity from intact cores for landslide soils (+) and understorey soils (x) are shown for comparison.

lishment usually limits the colonization of landslides by *Alchornea*. In the understoreys mortality rates were higher, at least for *Alchornea* and *Vaccinium*, as might be expected for gap-demanding species transplanted into shady microsites. *Clethra* survived equally well on landslides and in the understoreys, suggesting that its rarity in the understorey may be a result of the failure to establish where there is a litter layer.

Mortality in the dry season increased significantly for *Alchornea* and *Vaccinium* in the understoreys, but not on landslides. This is correlated with the marked drying of the soil in the understoreys (but not the landslides) in the dry season, which can be attributed to water uptake by the roots of canopy trees. The absence of a dry season effect on *Clethra* mortality suggests that it is more tolerant of drought, perhaps as an adaptation to more drought-prone elevated microsites (Newton & Healey 1990).

Mean seedling growth rates in forest gaps (Healey 1990) were higher than median seedling growth rates on landslides for *Alchornea* (0.36 cf. 0.13 mm day⁻¹) and *Clethra* (0.28 cf. 0.21 mm day⁻¹); mean seedling growth rates are likely to have been more reduced by

Alchornea which was almost entirely absent from the naturally regenerating flora of landslides (Dalling 1994). This suggests that dispersal or early estab-

small suppressed seedlings than the median growth rates, thus if strictly comparable results were used the differences would have been greater. Thus light gaps with forest soil are a more suitable environment for seedling growth than landslides.

IMPORTANCE OF NUTRIENT LIMITATION, SOIL MOISTURE AND SITE STABILITY

Growth is nutrient limited on landslides because: seedlings grow faster in gaps; seedling biomass or leaf area was increased by fertilization on landslides; soil nutrient concentrations are lower on landslides; and foliar nitrogen concentrations were lower on landslides than understoreys.

The major limiting nutrients on landslides are difficult to identify because nutrients were not applied separately, and because species responded to nutrient additions differently. All three species showed some increase in biomass with fertilization, with the greatest response from *Alchornea*. Biomass increases however, were modest, and there were no significant effects on seedling height growth. The unresponsiveness of *Clethra* and *Vaccinium* might be related to their age at the time of transplanting, or to the fact that these species naturally regenerate on landslides and may be insensitive to variations in soil nutrient availability. It is likely that N is a major limiting nutrient because foliar N concentrations in *Alchornea* were lower on landslides than in the understoreys. Possible nitrogen limitation on landslides is also suggested by the small pool of available nitrogen, low rate of N mineralization, and the low organic matter content of landslide soil. Even in sites where top soil is present, mature trees increased trunk growth following nitrogen fertilization (Tanner *et al.* 1990); loss of top soil is likely to exacerbate nitrogen limitation. However, the hypothesis that nitrogen is a major limiting nutrient on landslides needs to be tested by a field experiment.

In the understorey, shade and root competition are probably most important in suppressing seedling growth (Wilkinson 1939; Christy 1986). In general, fertilizer applications have failed to produce positive growth responses in seedlings growing in the understorey (Denslow *et al.* 1990; Turner *et al.* 1993), probably because plants in deep shade cannot make use of extra nutrients when they are strongly limited by low PAR. In fact the result in this experiment was a trend to reduced seedling growth following fertilization in the understoreys, probably due to roots from the canopy trees proliferating in the pockets of fertilizer to the detriment of the seedlings.

The low variation in soil water content through the year in landslides I, III and V, plus the fact that on at least one occasion during the year soil water measurements were made just after prolonged rains (so that soils were at, or above field capacity) implies that there was little deviation from field capacity throughout the

year, and thus that water was always in abundant supply on landslides. Measurements of stomatal conductance during dry periods would be needed to confirm that the plants were always well supplied with water.

Thus we have shown that growth of seedlings on landslides is limited by nutrient supply; water supply and soil movement do not limit growth of established seedlings. In the understorey, seedling growth is limited by photosynthetically active radiation (Healey 1990), nutrient supplies may limit seedling growth due to root competition, and seasonal drought is correlated with increased mortality. Further experiments should examine the importance of site factors on establishment on landslides, and the importance of root competition in the understorey.

Acknowledgements

This study was funded by a NERC studentship, and Frank Smart studentship to J. W. Dalling, and Smithsonian Mellon Fellowship to E. V. J. Tanner. Permission to carry out this study was given by the Department of Forestry, Government of Jamaica. The Director of Public Gardens, Ministry of Agriculture generously provided use of the Cinchona Botanic Gardens as a field base, and Prof. G. Sidrak, Dr D. Prasad, and Dr S. Iremonger of the Department of Botany, University of West Indies provided valuable assistance and facilities. We especially thank P. Bellingham, L. Burns, R. Kerr, H. Scrase, T. Mitchell and T. Goodland for help in the field, and P. Bellingham, J. R. Healey, and M. R. Guariguata for helpful advice in the preparation of this article.

References

- Adams, C.D. (1972) *Flowering Plants of Jamaica*. University of the West Indies, Mona, Jamaica
- Adams, P.W. & Sidle, R.C. (1987) Soil conditions in three recent landslides in S.E. Alaska. *Forest Ecology and Management*, **18**, 93–102.
- Anderson, J.M. & Ingram, J.S. (1989) *Tropical soil biology and fertility: A handbook of methods*. C.A.B. International, Wallingford, UK
- Christy, E.J. (1986) Effect of root competition and shading on growth of suppressed Western Hemlock. *Vegetatio*, **65**, 21–28
- Dalling, J.W. (1992) *Regeneration on landslides in the Blue Mountains, Jamaica*. PhD dissertation submitted to the University of Cambridge, UK.
- Dalling, J.W. (1994) Vegetation colonization of landslides in the Blue Mountains, Jamaica. *Biotropica*, **26**.
- Denslow, J.S., Schultz, J.C., Vitousek, P.M. & Strain, B.R. (1990) Growth responses of tropical shrubs to treefall gap environments. *Ecology*, **71**, 165–179.
- Flaccus, E. (1959) Revegetation of landslides in the White Mountains, New Hampshire. *Ecology*, **40**, 692–703.
- Garwood, N.C. (1985) Earthquake caused landslides in Panama: Recovery of vegetation. *National Geographic Society Research Reports*, **21**, 181–183.
- Grubb, P.J. & Tanner, E.V.J. (1976) The montane forests

- and soils of Jamaica: a reassessment. *Journal of the Arnold Arboretum*, **57**, 314–367.
- Guariguata, M.R. (1990) Landslide disturbance and forest regeneration in the Upper Luquillo Mountains. *Journal of Ecology*, **78**, 814–832.
- Healey, J.R. (1990) *Regeneration in a Jamaican montane tropical rain forest*. PhD dissertation submitted to the University of Cambridge, UK.
- Herwitz, S.R. (1981) *Regeneration of Selected Tree Species in Corcovado National Park, Costa Rica*. University of California Press, Berkeley.
- Kapos, V. & Tanner, E.V.J. (1985) Water relations of Jamaican montane rain forest trees. *Ecology*, **66**, 241–250.
- Nakamura, T. (1984) Vegetational recovery of landslide scars in the upper reaches of the Oi river, Central Japan. *Journal of Japanese Forestry Science*, **66**, 328–332.
- Newton, A.C. & Healey, J.R. (1989) Establishment of *Clethra occidentalis* on stems of the tree-fern *Cyathea pubescens* in a Jamaican montane rain forest. *Journal of Tropical Ecology*, **5**, 441–445.
- Shimokara, E. (1984) Natural recovery process of vegetation on landslide scars and landslide periodicity in forest drainage basins. *Proceedings of the Symposium on Effects of Forest Landuse on Erosion and Soil Stability, University of Hawaii, May 1984*.
- Stewart, G.H. (1986) Forest dynamics and disturbance in a beech/hardwood forest in Fiordland New Zealand. *Vegetatio*, **68**, 115–126.
- Sugden, A.M., Tanner, E.V.J. & Kapos, V. (1985) Regeneration following clearing in a Jamaican montane forest: results of a ten year study. *Journal of Tropical Ecology*, **1**, 329–351.
- Tanner, E.V.J. (1977) Four montane rain forests of Jamaica: Quantitative characterization of floristics, soils and foliar mineral levels. *Journal of Ecology*, **65**, 883–918.
- Tanner, E.V.J., Kapos, V., Freskos, S. & Healey, J.R. (1990) Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *Journal of Tropical Ecology*, **6**, 231–238.
- Turner, I.M., Brown, N.D. & Newton, A.C. (1993) Effect of fertilizer application on dipterocarp seedling growth and mycorrhizal infection. *Forest Ecology and Management*, **57**, 329–337.
- Varnes, D.J. (1958) Landslide type and processes. *HRB Special Report* (eds E. B. Eckel), pp. 20–47.
- Veblen, T.T. (1979) Structure and dynamics of *Nothofagus* forests near timberline in south-central Chile. *Ecology*, **60**, 937–945.
- Veblen, T.T. & Ashton, D.H. (1978) Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio*, **36**, 149–167.
- Whitmore, T.C. (1975) *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford.
- Wilkinson, G. (1939) Root competition and silviculture. *Malayan forester*, **8**, 11–15.
- Zar, J.H. (1984) *Biostatistical Analysis*. Prentice Hall, London.

Received 27 July 1993

Revised version accepted 23 March 1994