average values of the model parameters c and x are used, which is likely to involve some errors in the prediction.

Nonetheless, the predicted hydraulic conductivity of soils of the study area based on the model as proposed by Arya and Paris[11], was in satisfactory agreement with the measured values of the same. Similar results have also been reported[16]. However, there is scope for further improvement of the model by introducing factors that influence flow processes in soil under unsaturated moisture regime.

The results show considerable success in predicting hydraulic conductivity from PSD data of soils. The average values of the model parameters for a particular textural class were used in the study. As there are variations among the soil samples even within a specific textural class, attributed to differences in bulk density, organic matter content and mineralogical composition, textural similarities could not necessarily be translated into hydrophysical similarities. Some degree of disagreement observed between the predicted and the measured data suggests that the model needs further improvement to include some parameters, which influence the flow behaviour of the soils. Besides the present model, other PSD models have also been proposed and hence attempts to quantitatively investigate the effect of the choice of a PSD model on the prediction of $\psi(\theta)$ and $K(\theta)$ curves have been suggested[19].

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Impact of tsunami on terrestrial ecosystems of Yala National Park, Sri Lanka

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Yala National Park in southeast Sri Lanka, lay in the direct path of the December 2004 tsunami, hence afforded a rare opportunity to study tsunami impacts on a natural ecosystem. We surveyed the impacted area and studied the damage caused to vegetation, early response of vegetation, and effects on animals. Tsunami incursion was patchy, much of the coast being protected by sand dunes. Although impact on vegetation within inundated areas was intense, survival and resiliency of the flora were high. Recovery of vegetation will be rapid and mainly a process of regeneration

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rather than primary succession. Few large animals were impacted by the tsunami. The occurrence of any major long-term effects on fauna is unlikely.

Keywords: Ecological impact, Sri Lanka, tsunami, vegetation damage, Yala.

THE tsunami of 26 December 2004 caused widespread devastation in Asia, with a human death toll approaching 300,000 across eleven nations[1] and estimated economic losses over US$ 13 billion[2]. The tsunami impacted Sri Lanka approximately 1.5 h after its genesis, taking an estimated 30,000 lives[3] and causing extensive damage to anthropic environments.

Geomorphological effects and physical characteristics of the impacts of tsunamis[4–6] and destruction caused to society and built environments[7] have been well documented. However, few studies have examined their effects on natural terrestrial eco-systems[8]. The enormous forces exerted by tsunamis on coming ashore[9], and sea-water inundation extending inland over a scale of kilometres[10], create a unique environmental disturbance with few parallels. Termed a catastrophic salt-water inundation, the signature of past tsunamis can be detected even thousands of years later[11,12].

The coastal zone of Yala National Park (Figure 1) was surveyed on foot and data collected from 20 January to 2 April 2005. The inundation perimeter was identified from deposited debris and impacts on vegetation. GPS locations were recorded at approximately 50–100 m intervals along the perimeter, using hand-held GARMIN e-trex instruments. GPS data were superimposed on a geo-referenced MrSid image of a 1990 Landsat-4 satellite image, downloaded from https://zulu.ssc.nasa.gov/mrsid/. Areas were calculated on ArcView 3.2. Initial observations on vegetation were made six days after the tsunami, and vegetation data collected from 20 January 2005 to 11 February 2005 (25–47 days after the event). Line transects were conducted through the middle of incursions, from the beach to the inundation limit, in the direction of wave propagation. Damage to vegetation (grasses and herbs, shrubs, trees) was assessed in study plots centred on transect points at 100 m intervals.

Damage to grasses and herbs was assessed in 10 m radius circular plots. Each plot was assigned to one of five categories based on coverage: (i) all buried by sand, (ii) all dead or withered, (iii) most (> 50%) dead or withered, (iv) few (≤ 50%) dead or withered, and (v) none dead or withered. The first two categories were lumped for analysis. Regeneration and growth of new grasses and herbs were recorded in each plot.

Shrub damage was assessed in 20 m radius circular plots. The presence or absence of each of the four categories of effects on the shrubs was recorded in each plot: (i) completely uprooted (possibly deposited by the tsunami), (ii) partly uprooted or flattened, (iii) standing, but defoliated and (iv) undamaged. The presence or absence of new growth was noted in each plot.

Tree damage was assessed in 40 m × 100 m plots with the long axis parallel to the beach. Trees were divided into four size classes based on trunk circumference measured at the base[13] (16–30, 31–50, 51–100, > 100 cm). The presence or absence of each of the four categories of trees in each size class was recorded in every plot: (i) completely uprooted (possibly deposited by the tsunami), (ii) partly uprooted or flattened, (iii) broken (only basal part of the trunk standing), and (iv) standing. Defoliation and the presence or absence of new growth was noted for each recorded partly uprooted or standing tree.

Sixteen line transects were conducted, consisting of 122 transect points. To assess the relationship of damage to vegetation and distance from the sea, data from three distance categories (i) proximal to beach, (ii) mid transect and (iii) distal end of inundated area, were compared. For transects < 600 m length ($N = 6$), the first, middle and last study plots (e.g. 100, 300, 500 m) and for transects ≥ 600 m ($N = 10$), the first two, middle two and last two study plots (e.g. 100, 200; 600, 700; 1100, 1200 m) were used. All transect points were used for the other analyses. Chi-square tests were conducted to test for significance in differences.

Effects on fauna were assessed opportunistically. Any remains of dead animals were recorded.

The coastline of Yala National Park impacted by the tsunami was approximately 48 km. It consisted of a series of shallow bays and coastal dunes. Sea incursion by the tsunami occurred where dunes were deficient, as in lagoon or river outlets (Figure 1). Fifteen such major incursions

Figure 1. Satellite image of southern Sri Lanka. The area inundated by the tsunami shown in red. The major incursions are numbered. 1, Gode Kalapuwa; 2, Kuda-seelawa; 3, Maha-seelawa; 4, Uraniya; 5, Buttuwa; 6, Beeri-kalapuwa; 7, Pattanangala; 8, Gonelabba; 9, Kalliya; 10, Yala-wela; 11, Pilinnawa; 12, Pottana; 13, Gajabawa; 14, Gajaba-eliya and 15, Kumbukkan-oya estuary. (Inset) Map of Sri Lanka with enlarged area marked by white square.

were identified, seven of them discrete, with confluence from lateral flow behind coastal dunes in the rest (Figure 1). The total area inundated in Yala was 17.9 km^2 (including lagoons). Above-ground tsunami heights estimated from tree damage, rafted debris and dune scouring, ranged from 4.8 to 9.2 m ($\bar{x} = 6.28$, SD = 1.56, $n = 7$). Line transects through each of the major incursions found many large broken and uprooted trees, indicative of intense wave force. Observations included a gbh (girth breast height) of 298 cm for the largest broken and 330 cm for the largest completely uprooted tree, and a tree gbh 226 cm, uprooted and deposited 1100 m inland. Inundation distances (the furthest distance from shore to inland limit of flooding) in incursions ranged from 392 to 1490 m ($\bar{x} = 851.9$, SD = 366.7, $n = 10$). The main habitats affected were scrub forest and grasslands. Impacts on vegetation could be divided into physical effects from wave force and sand deposition, and physiological effects from salt-water inundation.

Grasses and herbs were heavily impacted, with 96% of 118 study plots having grasses and herbs showing damage. At the scale examined, the occurrence of damage was not related to distance from the sea (Figure 2 *a*), as high salinity caused the death of herbs and withering of above-ground parts of grasses over the entire area inundated. The severity of damage was related to distance from the sea, with significantly more damage observed in plots closer to the sea (few dead category: distal > mid or proximal, $P < 0.05$), due to sand deposition, greater wave force and possible inundation by multiple waves. As most short grass habitats in Yala occurred in the coastal zone, a large fraction of this was damaged by the tsunami. Recovery of grasses and herbs was high, with 96% of plots with damage showing recovery, and was independent of distance from the sea (Figure 2 *b*).

Shrubs were heavily impacted, with 84% of 86 study plots with shrubs showing damage. Shrubs were affected by both salt-water inundation (70% plots had defoliated-standing shrubs) and wave force (58% of plots had partially uprooted shrubs). Similar to grasses and herbs, at the scale examined the occurrence of damage from inundation (defoliation) was not significantly related ($P > 0.05$) to distance from the sea (Figure 2 *c*). Damage to shrubs from wave force was significantly related to distance from the sea (partially uprooted: distal < mid or proximal, $P < 0.05$; Figure 2 *c*). No significant difference was observed in the 'completely uprooted' category, possibly due to confounding from transport of uprooted shrubs inland by the wave.

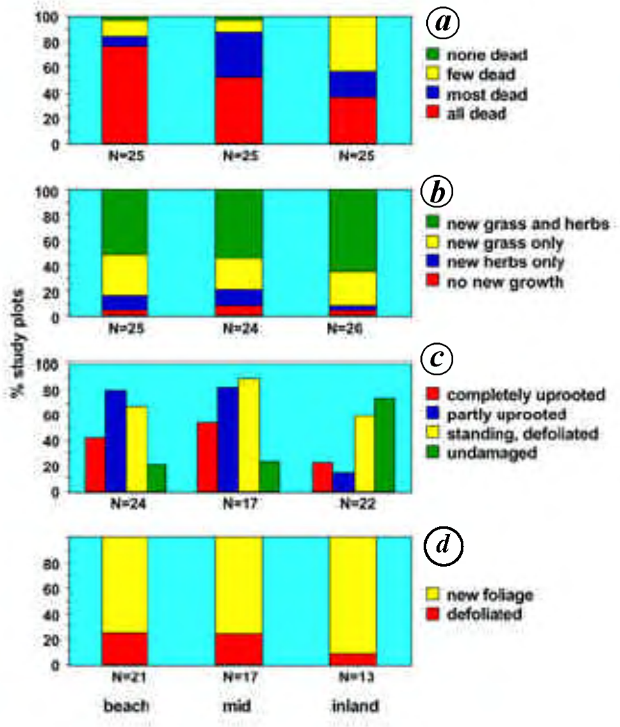

Figure 2. Damage to (*a*, *c*) and recovery (*b* and *d*) of grasses and herbs, and shrubs.

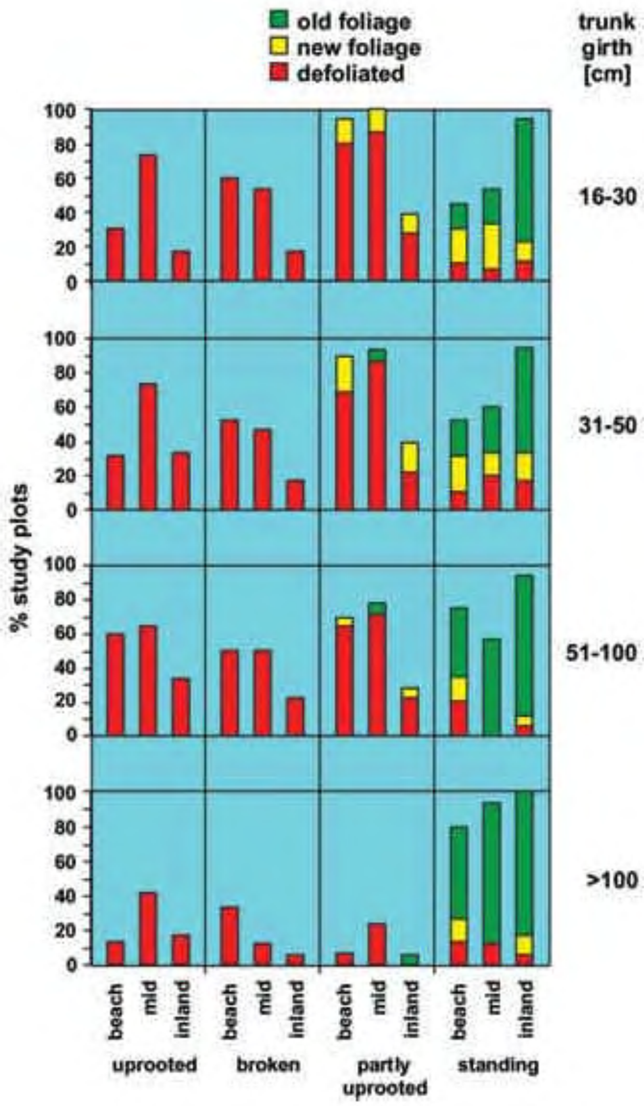

Figure 3. Damage to and recovery of trees.

Recovery of shrubs was high but less than in grasses and herbs, with regeneration of damaged shrubs in 79% of 72 plots. Regeneration was not significantly related to distance from the sea ($P > 0.05$; Figure 2 *d*).

The impact of the tsunami on trees was high, with 73% of 81 study plots with trees showing damage from wave force (59% had broken trees, and 69% had partly uprooted trees; Figure 3). Damage from salt-water inundation was also observed with 30% of 205 standing trees being defoliated. Tree damage was significantly related to distance from the beach (partially uprooted: proximal or mid > distal, $P < 0.05$; broken: proximal or mid > distal, $P < 0.05$; standing: distal > proximal or mid, $P < 0.05$) (Figure 3). Damage from wave force was related to size, with partial uprooting and breaking of trees of girth >100 cm being significantly less ($P < 0.05$) than those of smaller girth (Figure 3). As the canopy presents a large surface area, trees whose canopies were submerged by the wave were more likely to break or be uprooted. Larger trees withstood the wave force better, due to their structural robustness and the greater likelihood of their canopies being beyond the reach of the wave. Regeneration of standing but defoliated trees ($n = 63$) was moderate, with 54% showing new growth. Only a few (3%) of 148 partially uprooted trees retained their foliage. The rest were defoliated, with a small fraction (14%) showing regeneration. Completely uprooted trees did not show signs of regeneration and are unlikely to recover.

The onset of regeneration in grasses, shrubs and trees was observed days to weeks after the impact. Although logistics and time constraints prevented specific assessment, there appeared to be species differences in survival and recovery. Such variance, if associated with heritable attributes of species and individuals within species, could result in selection and hence adaptation[14]. Small tsunamis occur at a periodicity of decades in the South Asian region[15]. Major tsunamis occur more rarely at intervals of centuries[15], with the last one recorded[16] in Sri Lanka caused by the cataclysmic explosion of Krakatoa in 1883. The comparatively common occurrence of tsunamis on an evolutionary timescale of millions of years could make them an important evolutionary force in coastal floral communities.

A few freshwater bodies were swamped by the tsunami and turned saline. However, such water bodies were still used by water buffalos for wallowing, and crocodiles and fish were observed in them. As sea-water incursion was patchy, most coastal freshwater bodies were unaffected. Consequently, the tsunami did not have any significant effect on the availability of freshwater for animals in Yala.

The remains of a few animals that died from the tsunami, such as water buffalo ($n = 2$), wild boar ($n = 1$), spotted deer ($n = 1$), hare ($n = 1$), peacocks ($n = 2$), herons and cormorants (fledglings in nests), python ($n = 1$), sea turtles ($n = 2$), and star tortoises ($n = 4$), were observed within inundated areas. Dead land snails of many species were observed over the entire inundated area. Groups such as small mammals, lizards and especially those intolerant to salt water such as amphibians, snails and earthworms are likely to have been heavily impacted. However, given their large population sizes, it is unlikely to be of significance at species level. The tsunami also damaged a large fraction of short grass habitat in Yala at the height of its productivity. However, the rapid recovery of grasses, and the absence of obligate grazers, predicts minimal long-term effects on herbivores. Thus, most fauna appeared not to have been heavily impacted by the tsunami.

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