Downloaded from rstb.royalsocietypublishing.org

# Interesting times on Krakatau: stand dynamics in the 1990s

Robert J. Whittaker, Tukirin Partomihardjo and Stephen H. Jones

*Phil. Trans. R. Soc. Lond. B* 1999 **354**, 1857-1867
doi: 10.1098/rstb.1999.0527

**Email alerting service** Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: **http://rstb.royalsocietypublishing.org/subscriptions**

This journal is © 1999 The Royal Society

Downloaded from rstb.royalsocietypublishing.org

THE ROYAL SOCIETY

# Interesting times on Krakatau: stand dynamics in the 1990s

**Robert J. Whittaker**[1]*, **Tukirin Partomihardjo**[2] **and Stephen H. Jones**[1]

[1]*School of Geography, University of Oxford, Mansfield Road, Oxford, OX1 3TB, UK*
[2]*Herbarium Bogoriense, Jalan Ir. H. Juanda 22, Bogor 16122, Indonesia*

The Krakatau Islands, Indonesia, have provided an opportunity for ecologists to track primary succession from the 'clean slate' of 1883, through forest closure in the 1920s, to the contemporary period, in which successional changes take the form of alterations in composition and stature of forest stands rather than gross changes in ecosystem type. This paper reports on permanent forest plots established on the islands in 1989, and fully surveyed again in both 1992 and 1997. Since 1989, the plots have been subject to natural disturbance phenomena in the form of varying combinations of, for example, deposition of volcanic ejecta, landslides, lightning strikes, storm damage and drought. These effects have been concentrated between 1992 and 1997, during which the volcano Anak Krakatau has deposited ash on the islands of Sertung and Panjang, but not on Rakata. Data on stand responses are presented for growth rates (dbh (diameter at breast height, 1.3 m) increment), stem recruitment and mortality, biomass changes (partitioned into mortality, ingrowth and growth of established trees), and compositional shifts. The discussion focuses on evaluation of questions and successional models framed earlier in the programme. One general finding is that the stand dominants as of 1989 have tended to decline in number within the plots, generally through low levels of recruitment failing to balance rates of mortality. The effects of disturbance to the plots appear to be evident in terms of mortality and recruitment, dbh increment, and changes in biomass. The patterns of change in the eight plots are quite varied, such that relatively few generalizations are possible. The difficulties of establishing meaningful baseline rates for tree growth and stand biomass are discussed.

**Keywords:** Krakatau, Indonesia; succession; forest ecology; stand dynamics; disturbance ecology

## 1. INTRODUCTION

The 1990s have been interesting times on Krakatau in the sense that the forests we have been monitoring have been buffeted by droughts and storms, and have had varying amounts of volcanic ash deposited on them, breaking stems and branches, and covering the foliage of the trees in an opaque, often persistent layer (Schmitt & Whittaker 1998). They have been times when, for a forest tree, there may have been more favourable places to have taken root. The aim of this paper is therefore to describe the dynamics of permanent forest plots in a period of seemingly high rates or intensities of natural disturbance. However, the previous empirical and theoretical work undertaken on Krakatau allows us to go a little beyond description, and to attempt an evaluation of our earlier predictions concerning both the successional trends and the response of the forests to disturbance.

In 1883, Krakatau (6°06′ S, 105°25′ E) consisted of three islands arranged in a caldera, located in the Sunda Strait between Java and Sumatra. Having been dormant since 1680, the largest island in the group began a sequence of eruptions in May of 1883 that ended on 27 August of that year in exceptionally destructive eruptions. Two-thirds of that island disappeared, vast quantities of ejecta were thrown into the atmosphere, and a series of huge waves (tsunami) generated in the collapse of the island resulted in an estimated 36 000 human casualties in the coastal settlements of Java and Sumatra flanking either side of the Sunda Strait some 40 km from Krakatau (Simkin & Fiske 1983; Thornton 1996). Each of the three Krakatau islands was entirely stripped of all vegetation. The main island, now known as Rakata, lost the majority of its land area, but all three islands also gained extensive areas of new land resulting from the emplacement on to the pre-existing solid rock bases of great thicknesses of pyroclastic deposits. Estimates of the ash depths deposited are of the order of 60–80 m and to this day most of the surface area of the three islands remains mantled in these unconsolidated ashes, with very little solid geology exposed at the surface. After the eruptions, no evidence for any surviving plant or animal life was found by the scientific team led by R. D. M. Verbeek in October 1883, and in May 1884 the only life spotted by visiting scientists was a spider. The first signs of plant life, a 'few blades of grass', were detected in September 1884. While it is conceivable that some plant propagules might somehow have survived to be uncovered by later erosion of the ash mantle (Whittaker *et al.* 1995), there is no evidence of survival, and indeed the densest populations of early plant colonists were located on *terra nova*. The islands can be taken to

---

[*] Author for correspondence (robert.whittaker@geography.oxford.ac.uk).

© 1999 The Royal Society

Downloaded from rstb.royalsocietypublishing.org

have been as near completely sterilized as makes no practical difference (see accounts in Docters van Leeuwen 1936; Simkin & Fiske 1983; Whittaker *et al.* 1989; Thornton 1996).

The present-day fauna and flora of Krakatau have thus colonized since 1883 from an array of potential source areas, the closest of which, the island of Sebesi, is 12 km distant. All the nearest land areas, including Sebesi, were also badly impacted by the 1883 eruptions (Docters van Leeuwen 1936). The great potential of the islands as a natural experiment in dispersal efficacy and ecosystem recovery was appreciated at an early stage and the development of the vegetation and the flora have been monitored—albeit intermittently and with varying degrees of precision—since M. Treub's survey of 1886 (e.g. Ernst 1908; Docters van Leeuwen 1936; Whittaker *et al.* 1989, 1997). While the present paper is restricted in focus to forest dynamics, recent studies have covered a wide variety of topics, including recolonization by animals (e.g. Thornton *et al.* 1990; Thornton 1996), relevance of island biogeographical theories (e.g. Bush & Whittaker 1991, 1993; Thornton *et al.* 1993; Whittaker 1998), plant–animal interactions (e.g. Compton *et al.* 1994; Whittaker & Jones 1994*a*,*b*; Bush *et al.* 1995; Shilton *et al.* 1999) and soil development (e.g. Schlesinger *et al.* 1998).

Succession in the strand-lines was relatively simple and fast, with the first woodlands—dominated by sea-dispersed plants—soon establishing behind the beaches and thereafter not changing greatly in general composition. Inland, the first higher plant colonists were ferns, grasses and composites, all being wind-dispersed taxa. An increasingly dense grassland cover developed, but from around the end of the 19th century, bird- and bat-dispersed trees and shrubs established within these 'open' habitats, forming isolated clumps. These gradually coalesced such that by about 1930 the lowland interiors of the islands were each covered by broadly similar, species-poor, closed tropical forest (Docters van Leeuwen 1936; Whittaker *et al.* 1989; Whittaker & Jones 1994*a*,*b*).

At a more detailed level, some differences were apparent around 1930 between the vegetation of Rakata and the other two islands, Panjang and Sertung. These appeared to relate to variations in environment, and to chance differences in landfall of the initial colonizing populations (Docters van Leeuwen 1936). Significantly, 1930 was also the year in which renewed volcanism (initiated in 1927) led to the establishment of a new island, Anak Krakatau, in the centre of the Krakatau caldera. It soon began to have visible effects on the forests of Panjang and Sertung, but not apparently on Rakata, which appears to have escaped damaging ash deposition because it does not lie windward of Anak Krakatau in either the wet or dry seasons (Whittaker *et al.* 1992*b*).

Since the 1930s, most of the interior of Rakata up to about 500 m, has been covered in forest dominated numerically by *Neonauclea calycina* (nomenclature follows Backer & Bakhuizen van den Brink 1963–1968 and Whittaker *et al.* 1989), an early-successional wind-dispersed tree. From about 500 m to the summit at *ca.* 750 m, a further distinctive submontane forest type is found (Whittaker *et al.* 1989). Panjang (142 m elevation) and Sertung (182 m elevation) lack upland habitats, and as recognized in the 1980s, they share two principal inland forest types, dominated respectively by *Timonius compressicaulis* and *Dysoxylum gaudichaudianum*. This description is a considerable simplification, as first, other stand types may be recognized on the basis of dominance (e.g. stands recently described on Panjang in which *Neonauclea calycina* and *Timonius compressicaulis* share numerical dominance; Schmitt & Whittaker 1998), and second, with an inland tree flora of over 70 species, unsurprisingly the forests vary greatly in compositional detail across each island (Schmitt 1997).

Forest ecological analyses, based mostly on temporary forest plot data collected between 1979 and 1983, generated differing views on the dynamics of the main inland forest types of the islands, and of the relevance of particular environmental factors (chiefly disturbance and edaphic variation) and biotic factors (autecology and dispersal constraints) in influencing these dynamics (e.g. Tagawa *et al.* 1985; Whittaker *et al.* 1989; Bush *et al.* 1992; Tagawa 1992). Tagawa *et al.* (1985) stressed the significance of timing of arrival and edaphic constraints in explaining the contemporary vegetation patterns, whereas Whittaker *et al.* (1989) and Bush *et al.* (1992) placed more emphasis on the role of disturbance by volcanism, suggesting that the link between soil properties and forest distribution was a result of disturbance history rather than a reflection of underlying edaphic heterogeneity. They suggested that over large areas of Sertung and Panjang, disturbance had reset succession (variably in space and time). At least partly in response to such opportunities, *Timonius compressicaulis* had formed extensive stands, typically, or at least often, to be succeeded by the taller *Dysoxylum gaudichaudianum*.

Although Krakatau provides a singular data series for the humid tropics, it was not until 1989 that the first permanent plots were established to monitor quantitatively the dynamics of the forests (Bush *et al.* 1992). At that time, a good general picture of the historical succession and contemporary forest types on Krakatau had been established, but there were no systematic data pertaining to growth rates, recruitment rates, mortality rates, and thus turnover of forest stands, either for Krakatau itself or (to our knowledge) for any other forests in adjacent provinces of Java and Sumatra. Moreover, as already noted, there were some differences of interpretation regarding the recent forest dynamics and likely future pathways of succession (e.g. compare Tagawa *et al.* 1985 and Whittaker *et al.* 1989). The general goals of the permanent plots programme were thus as follows. First, to measure growth and turnover rates for the main types of inland forest. Second, to monitor compositional changes in the plots in order to better describe the succession and to discriminate between the differing models of succession that had been put forward. Third, through this to improve our scanty knowledge of the key processes at work, and of the autecology of at least the commoner tree species of Krakatau. Six plots were established in 1989, and two more were added during a complete resurvey in 1992. Mortality data were recorded from all but one of the plots in 1994–1995 in order to document an episode of stand disturbance (Whittaker *et al.* 1998), and a full resurvey of all eight plots was undertaken in 1997, reported herein.

Downloaded from rstb.royalsocietypublishing.org

### (a) *Specific issues addressed*

#### (i) *Compositional change*

First, it was expected that Rakata would feature a gradual reduction in the extensive monodominance of *Neonauclea calycina*, either to be succeeded by forest dominated by *Dysoxylum gaudichaudianum* (see Tagawa *et al.* 1985), or with a distinct trend from the general Krakatau pattern of monodominance towards a more diverse set of successionally more advanced canopy species (see Whittaker *et al.* 1989; Bush *et al.* 1992).

Second, based on the historical activity of Anak Krakatau and what was known of its impact on the other islands, we expected that future volcanic eruptions would occur and that they would impact differentially on Sertung and Panjang as opposed to Rakata (as indeed happened during 1992–1997). The permanent plots would thus allow monitoring of forest responses to disturbance. We anticipated (see Whittaker *et al.* 1989) that in such an event, *Timonius compressicaulis* would be one of those species that would show a capacity to recruit into sites disturbed by volcanism.

Third, following on from the second point, we were interested to see if *Dysoxylum gaudichaudianum* would show a capacity to grow through and dominate the canopy in sites initially filled by *Timonius compressicaulis*.

#### (ii) *Changes in diversity*

We anticipated that chronic disturbance would depress within-stand diversity, whereas 'normal' gap dynamic processes would be instrumental in increasing stand diversity, within the broader context of islands that continue to accrue new colonists (Bush *et al.* 1992; Whittaker *et al.* 1989, 1992*a*).

#### (iii) *Growth responses and stand biomass*

Following observations by Bush *et al.* (1992), we expected that chronic disturbance would depress growth and standing biomass in the short term, but where leading to the formation of large gaps, would allow ingrowth and relatively rapid growth of surviving trees once the disturbance event had ended.

## 2. MATERIAL AND METHODS

### (a) *Study area*

The climate of the Krakatau islands has been classified as Afa in the Köppen's world system (i.e. a tropical rainy climate with a few dry months), with annual precipitation estimated to lie between 2500 and 3000 mm, and mean monthly temperature varying between 26.9 and 28.7 °C for 1929, the one year for which a full set of readings is available (Whittaker *et al.* 1989, 1998). The dry season between May and October can be extreme, such that sites may receive no rain for several successive weeks in July–September. In this region, inter-annual variations in rainfall, and in particular in the intensity and duration of the dry season, are linked to El Niño Southern Oscillation (ENSO) events, wherein extreme dry seasons (El Niño) are often followed by heavy rains (La Nina) (e.g. Nicholls 1991; Walsh 1996, this issue). The early 1990s was a period of unusually intensive ENSO activity, and during 1994, for instance, almost no rain fell in the Krakatau area for about five months. Evidence from studies of gap dynamics on the islands around 1993–1995 indicates that both drought and storm damage were significant influences on mortality, growth and recruitment patterns during the study period considered herein (Schmitt & Partomihardjo 1997; Schmitt & Whittaker 1998; Whittaker *et al.* 1998). Similarly, the period 1992–1997 was one of extensive damaging ash fall on Panjang and especially on Sertung. When the permanent plots programme was initiated in 1989, there had been negligible volcanic activity for about eight years, but immediately after the 1992 resurvey, Anak Krakatau commenced a renewed phase of activity lasting the duration of the present study (Thornton *et al.* 1993; Schmitt & Whittaker 1998; Whittaker *et al.* 1998).

### (b) *Sample sites and methods*

The aims at the outset were to represent the major forest types as previously identified using detrended correspondence analysis (ordination) and TWINSPAN (multivariate classification) analysis of 35 temporary plots (Whittaker *et al.* 1989), and to sample each island. As Rakata mostly consisted of forest dominated by *Neonauclea calycina*, we initially set up one low (R1) and one mid-altitude *Neonauclea* stand (R2), adding in 1992 another low altitude *Neonauclea*-dominated plot (R4) and a high altitude plot (R3) dominated by *Saurauia nudiflora*. Panjang and Sertung each featured stands dominated by *Timonius compressicaulis* (P2, S2) and also extensive *Dysoxylum gaudichaudianum*-dominated stands (P1, S1): accordingly, one plot was established in each forest type on both islands. Thus, as of 1989, we had two plots of each of the three main dominants, providing a degree of replication within the initial sampling design. In 1992, we resurveyed each of these plots and added the two additional Rakata plots. (For the sake of brevity, we refer to the dominants hereafter by their generic names only.)

The plots were located in more or less closed forest considered representative of the types previously identified, distant from the coastal zone, on the flattest, least dissected terrain available. In practice, the two upland Rakata plots have quite steep slopes, and none of the plots are entirely flat. Initially, plot areas of 30 × 30 m were laid out. A minimum of 100 trees was sampled from each plot, and the maximum number (initially) was 142. Where necessary, plots were extended in strips until the required sample sizes were obtained. The low diversity characteristic of the tree layer enabled adequate samples to be obtained of the commonest tree species within these relatively small plots (Bush *et al.* 1992). At each resurvey, the following data were recorded for all stems $\geqslant 5.0$ cm diameter at breast height (dbh, 1.3 m): (i) dbh, total height, height to first major leafing, canopy status and phenological status of previously enumerated individuals; (ii) the same, plus location and species of all individuals recruited into the tree layer; and (iii) specific notes on condition and/or mortality. Sapling data were also recorded but are not reported herein. Surveys were carried out during the dry season in July and August. Trees were marked using pre-punched aluminium tags, replaced as necessary on resurveys. The dbh of each tree was recorded using diameter-calibrated metric tapes. For trees with buttresses, diameter was measured both at the standard height and above the buttress to allow bridging of measurements (c.f. Alder & Synott 1992). In the analyses reported here, individual stems that cease to qualify as trees by dint of no longer having a dbh $\geqslant 5.0$ cm, even if remaining alive, have been treated as dead, i.e. they count as 'mortality'. Some individuals fall from the tree layer only to resprout, and at a later date to re-enter the tree layer, in which case they add both to mortality and subsequently to recruitment columns.

Values for above-ground biomass were estimated as a function of dbh and tree height, according to the formula recommended

Downloaded from rstb.royalsocietypublishing.org

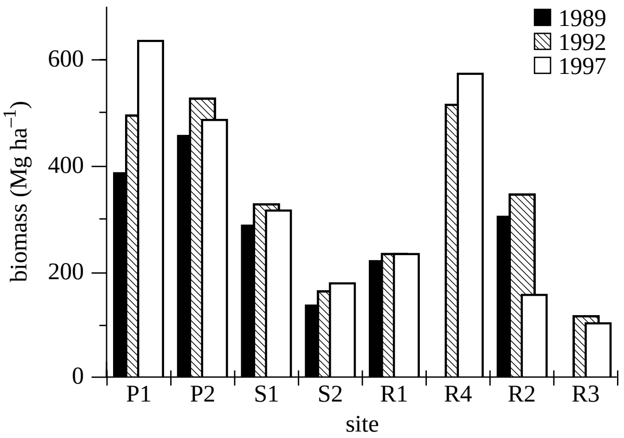

Figure 1. Standing biomass of all stems in the tree layer (defined as those $\geqslant$ 5.0 cm dbh) of each of the Krakatau permanent plots for 1989, 1992 and 1997. Plots: P1, Panjang plot 1 (area 1240 m$^2$); P2, Panjang plot 2 (area 900 m$^2$); S1, Sertung plot 1 (area 900 m$^2$); S2, Sertung plot 2 (area 900 m$^2$), R1, Rakata plot 1 (area 1760 m$^2$); R4, Rakata plot 4 (area 1272 m$^2$); R2, Rakata plot 2 (area 1200 m$^2$) and R3, Rakata plot 3 (area 440 m$^2$). The Rakata plots are arranged on the ordinate by altitude (see table 1 for further details). Values calculated according to the formula: biomass (Mg ha$^{-1}$) = 1.276 + 0.034(dbh$^2$ × height) (Brown & Iverson 1992). Most studies report values calculated on the basis only of trees $\geqslant$ 10 cm dbh (Gillespie *et al.* 1992), but we use the lower cut-off here as it preserves more information on stand dynamics. Accordingly, our values for 1992 differ slightly from those reported by Whittaker *et al.* (1998) using the 10 cm cut-off point.

for the moist-life zone (Brown & Iverson: 1992; S. Brown personal communication), wherein biomass (Mg ha$^{-1}$) = 1.276 + 0.034(dbh$^2$ × height). We use the data for biomass as a crude index of the stand stature over the course of the study, and also present data for the change in biomass resulting from mortality, the growth of pre-existing trees, and the ingrowth of recruits, as a means of assessing the underlying stand dynamics. However, as these data can be misleading in isolation, we are also present data for dbh increment, and for mortality and recruitment in terms of numbers of stems.

## 3. RESULTS

The volcano was inactive between the first two surveys of the plots in 1989 and 1992, but in November 1992, a series of eruptions began (Thornton *et al.* 1994) that continued with only short breaks into 1997, depositing ash extensively across Panjang and Sertung (Schmitt & Partomihardjo 1997; Whittaker *et al.* 1998). The plots on Rakata received no ash fall (and have not since 1883), but did experience storm damage, including lightning strikes to two of the plots during the 1992–1995 period. Considering only the six original plots (R1, R2, P1, P2, S1 and S2), the tree mortality rate for 1989–1992 was 3.1% yr$^{-1}$, which qualifies as background tree mortality (Lugo & Scatena 1996), and that for 1992–1995 was 7.4% yr$^{-1}$, thus qualifying as an episode of 'catastrophic' tree mortality (Whittaker *et al.* 1998). There was a noticeable shift to mortality of canopy and emergent trees in 1992–1995. Unfortunately, we do not have appropriate data to allow quantification of disturbance to our plots other than by reference to the vegetation itself. However, field observations support previous stratigraphical studies (Whittaker *et al.* 1992*b*) that indicated greater depths of ash fall in the vicinities of the two Sertung plots than the two Panjang plots. Moreover, during the dry season, when ash is less likely to be washed from the foliage, the prevailing winds carry ash to Sertung (Schmitt & Partomihardjo 1997), where it was observed over the 1993–1997 period to have caused great destruction and innumerable whole- or partial-tree falls.

Figure 1 shows how the standing biomass of the tree layer has changed during the eight years of the study in each plot (five years' data only for R3 and R4). There is a marked difference in trend between the two periods of the study, with all six sites sampled in 1989 increasing in biomass to 1992, whereas between 1992 and 1997 three sites increased in biomass, four decreased and one was unchanged. The figure is indicative of the considerable variation in tree density and stature within the islands. Beginning with Sertung, the *Timonius* plot, S2, had a particularly low initial biomass, and both it and the *Dysoxylum* plot, S1, began with lower values than the equivalent plots on Panjang (P2 and P1). Both have featured only a slight overall increase in biomass over the eight years. The Panjang *Timonius* plot, P2, increased in biomass from 1989 to 1992, and then declined slightly to 1997. The *Dysoxylum* plot, P1, however, has shown a substantial increase over both periods, to finish with the highest value of any in the study. On Rakata, similarly divergent patterns of change have occurred within the *Neonauclea* plots. R1 has changed little, whereas R4, which was first sampled in 1992, increased on a comparatively high baseline value, and the mid-altitude R2 underwent first an increase, and then a large decline. The fall occurred due to a gap created by a lightning strike and subsequent massive gap expansion, such that between 1992 and 1994 the biomass had fallen from 345 to 150 Mg ha$^{-1}$. A similar value, of 155 Mg ha$^{-1}$, was recorded in 1997. The final plot, the *Saurauia*-dominated plot in the summit region of Rakata, showed the lowest biomass value in 1992 and minimal change by 1997.

Underlying the patterns of change shown in figure 1, are a variety of different dynamics, such that, for instance, some of the plots showing least change in stand volume, have actually experienced very substantial turnover (table 1). In all six plots for which 1989 data were recorded, loss through mortality was higher in the 1992–1997 period than between 1989 and 1992, and in all but S1, the rate of loss per annum was also higher in 1992–1997. The increment in biomass arising from the growth of established trees in the six plots was at a greater rate per annum between 1989 and 1992 than between 1992 and 1997. Increment from recruitment was generally low, as would be expected given that all recruits are by definition small trees. The highest two values for ingrowth corresponded to the two higher altitude Rakata plots, R2 and R3, which each experienced massive losses following storm damage (involving lightning strikes) in 1992 and 1993. In the case of R2, 38% of the stems recorded in 1992 were dead by 1994, and in R3, 43% of the stems recorded in 1992 were dead by 1995. The higher values for biomass gain through ingrowth in these two plots is indicative of the large amounts of space thus created and the correspondingly

Downloaded from rstb.royalsocietypublishing.org

Table 1. *Biomass change in Krakatau permanent plots*

(Initial values for biomass for the year in which each site was set up, and components of change in Mg ha$^{-1}$, where change = growth + ingrowth − mortality.)

| plot | dominant | altitude (m) | period | initial | change | growth | ingrowth | mortality |
|---|---|---|---|---|---|---|---|---|
| Panjang 1 | *Dysoxylum gaudichaudianum* | 75 | 1989–1992 | 383 | 110.4 | 111.6 | 3.4 | −4.6 |
| | | | 1992–1997 | | 140.1 | 161.8 | 2.2 | −23.9 |
| Panjang 2 | *Timonius compressicaulis* | 130 | 1989–1992 | 455 | 70.9 | 77.6 | 0.9 | −7.6 |
| | | | 1992–1997 | | −41.9 | 24.5 | 4.8 | −71.2 |
| Sertung 1 | *Dysoxylum gaudichaudianum* | 80 | 1989–1992 | 283 | 40.2 | 67.2 | 2.0 | −49.0 |
| | | | 1992–1997 | | −10.5 | 34.4 | 6.6 | −51.5 |
| Sertung 2 | *Timonius compressicaulis* | 140 | 1989–1992 | 136 | 28.2 | 36.1 | 0.1 | −8.0 |
| | | | 1992–1997 | | 13.3 | 29.8 | 4.6 | −21.1 |
| Rakata 1 | *Neonauclea calycina* | 110 | 1989–1992 | 221 | 13.6 | 22.4 | 2.8 | −11.7 |
| | | | 1992–1997 | | −0.3 | 26.2 | 2.0 | −28.5 |
| Rakata 4 | *Neonauclea calycina* | 190 | 1992–1997 | 514 | 58.9 | 74.6 | 1.2 | −16.9 |
| Rakata 2 | *Neonauclea calycina* | 450 | 1989–1992 | 303 | 41.4 | 46.7 | 0.7 | −6.0 |
| | | | 1992–1997 | | −188.9 | 39.3 | 11.2 | −239.3 |
| | | | 1992–1994[a] | | −193.7 | 8.9 | 0.8 | −203.4 |
| | | | 1994–1997[a] | | 4.8 | 33.7 | 9.0 | −37.9 |
| Rakata 3 | *Saurauia nudiflora* | 680 | 1992–1997 | 116 | −14.2 | 17.8 | 25.5 | −57.5 |

[a] An additional full survey of Rakata 2 was carried out in 1994; these data show the catastrophic loss incurred between 1992 and 1994, and the subsequent slight recovery in biomass. The values for 1992–1997 cannot be derived simply from the 1992–1994 and 1994–1997 values because of changes in the status of a tree within the longer survey period.

Table 2. *Diameter increments of surviving stems in Krakatau permanent plots*

(Increments of dbh in cm yr$^{-1}$ for all stems > 5.0 cm dbh in both start and end year. *n* refers to the number of stems for which readings at time 1 and time 2 were available.)

| | | 1989–1992 | | | 1992–1997 | | |
|---|---|---|---|---|---|---|---|
| plot | dominant | growth | s.d. | *n* | growth | s.d. | *n* |
| Panjang 1 | *Dysoxylum* | 0.3516 | 0.7049 | 124 | 0.2517 | 0.3987 | 113 |
| Panjang 2 | *Timonius* | 0.1360 | 0.3780 | 138 | 0.1516 | 0.1850 | 119 |
| Sertung 1 | *Dysoxylum* | 0.2181 | 0.3478 | 105 | 0.2688 | 0.3031 | 86 |
| Sertung 2 | *Timonius* | 0.1260 | 0.1489 | 140 | 0.1588 | 0.1639 | 121 |
| Rakata 1 | *Neonauclea* | 0.3095 | 0.3630 | 97 | 0.2680 | 0.4900 | 100 |
| Rakata 4 | *Neonauclea* | — | — | — | 0.1198 | 0.2300 | 82 |
| Rakata 2[a] | *Neonauclea* | 0.2420 | 0.4990 | 94 | 0.5553 | 0.5506 | 47 |
| Rakata 3 | *Saurauia* | — | — | — | 0.3953 | 0.3066 | 47 |

[a] For Rakata 2, data are also available from a full survey of the site in 1994. Rakata 2, 1992–1994, mean = 0.4702, s.d. = 0.7002, *n* = 64. Rakata 2, 1994–1997, mean = 0.7367, s.d. = 0.7632, *n* = 50.

high rates of recruitment. In respect of the Panjang and Sertung plots, the growth element was greater in the *Dysoxylum* plots than the *Timonius* plots in each period. The Panjang plots also displayed more increment from growth than the Sertung plots; the only exception being provided by P2 in 1992–1997, when the growth increment was very similar in both *Timonius* plots. In P1 and S2, the loss of biomass through mortality was much greater in the 1992–1997 period, but in both periods the growth of established trees outweighed the losses. In P2 and S1, growth outweighed mortality between 1989 and 1992, but for 1992–1997 the reverse occurred.

The data in table 1 are standardized by area, and thus, in plots with a high mortality of large trees, there is a tendency for the growth component of biomass change to decline simply as a function of the reduced number of trees. Another means of examining growth of trees in these circumstances is to record the mean dbh increment of survivors (table 2). These data show that for the three plots where biomass first increased and then declined (P2, S1 and R2; figure 1), the surviving trees actually gained in diameter at a faster rate during the period of biomass loss. Moreover, with reference to table 1, it can be seen that the biomass increment from growth in each of these plots was also lower in the second period, when dbh increments were higher. This apparent contradiction is explicable as a function both of the reduction in the number of trees contributing to the biomass increment

Downloaded from rstb.royalsocietypublishing.org

from growth, and of the release of (mostly) smaller stems from competition. The latter may produce a high dbh increment without a correspondingly high increase in plot biomass (most of which is accounted for by the largest canopy trees or emergents). The detailed picture of stand dynamics provided by these differing summary data (tables 1 and 2; figure 1) reveals that no two plots have followed a common trajectory over the eight years of the study. The following accounts provide the detailed results for each site in turn.

### (a) *Sertung plot 1*

Plot S1 is dominated by *Dysoxylum*. In 1989, 90 out of the 124 stems (73%) in the plot were of this species. The respective figures for 1992 were 81 out of 124 (65%) and, for 1997, 70 out of 144 stems (49%). Altogether, 29 individuals of this species have died in the study period, and nine have recruited. While this would appear to signify a decline in the dominant species in the plot, in practice it remains the only canopy species, providing all 13 of the remaining trees of greater than 20 m height. The only two other potential canopy species of similar stature at maturity, *Ficus pubinervis* and *Buchanania arborescens*, are present only as single small trees. Moreover, the average mortality rate for the plot is slightly higher than that for *Dysoxylum* alone. Between 1989 and 1992 across all species, the plot experienced 14.5% mortalities (4.8% $\mathrm{yr}^{-1}$), and for 1992–1997 30.6% mortalities (6.1% $\mathrm{yr}^{-1}$)—which in turn was concentrated in the period 1992–1995. The losses post-1992 are principally due to volcanic disturbance in the form of ash deposition (leading to a general reduction in leaf volume and many broken trees and branches), with some additional evidence of lightning kills within and adjacent to the plot (Whittaker *et al*. 1998). A large tree-fall gap developed in the plot, accounting for many of the losses across all sizes of stem.

The recruitment into the plot, other than of *Dysoxylum*, has featured mostly understorey or early successional trees, the most abundant being *Gnetum gnemon* and *Piper aduncum*, and also including *Antidesma montanum*, *Macaranga tanarius* and *Ficus septica*. *Timonius* has not featured in the tree layer of the plot during the study. There were, however, seven *Timonius* saplings in a sample of 87 saplings recorded in 1992 (in a subplot): none survived to 1997 and the species did not appear to have recruited to the sapling layer between 1992 and 1997 in the area sampled. In 1989, there were 14 species in the tree layer in the plot; of these three were lost, with three others being recruited. In short, in this plot, everything has changed yet nothing has changed. A period of disturbance, accelerated turnover, of gap creation and gap fill, leaves the plot looking very different in terms of its architecture, but with a similar species complement, a similar biomass, and the same dominant species in a paramount position.

### (b) *Sertung plot 2*

Plot S2 is dominated by *Timonius*, which represented 124 out of 157 stems (79%) in 1989, 112 out of 150 (75%) in 1992, and 102 out of 153 (67%) in 1997. Many trees in the plot, particularly of the dominant, are multistemmed. During 1989–1992, 13 out of 15 mortalities from the plot were of this species, whereas between 1992 and 1997, the respective figures were 13 out of 28. This translates to 90% survivorship of *Timonius* from 1989 to 1992, and 88% survivorship from 1992 to 1997. The respective figures for all other species in the plot were 88 and 61%. Most of the *Timonius* that died between 1989 and 1992 were killed in a lightning strike. Subsequently, during the period of volcanic ash deposition, *Timonius* has suffered lower attrition than the rest have experienced collectively, and in 1997 it provided the only trees of ⩾ 20 m height in the plot. Despite the better survivorship, the dominant has a reduced proportion of the live stems, as a result of its negligible recruitment over the last eight years (one sapling in 1992, and three new stems to existing clumps by 1997).

While recruitment to the plot has balanced mortality in terms of number of stems in the plot, the gain in biomass has been very slight over the eight years, with the rate of gain and rate of dbh increment each being reduced over the 1992–1997 period of ash deposition. The plot contained only nine species in the tree layer in 1989, and the number was reduced to seven in 1997. They were: *Timonius*, three of the pioneer figs (*Ficus fistulosa*, *septica* and *fulva*), *Bridelia monoica*, *Terminalia catappa* (one individual) and *Dysoxylum*. The latter increased from three recently recruited trees in 1989 (2% of stems), to 13 by 1997 (9% of the stems). In a plot with negligible growth in biomass and low dbh increment, they were clearly exceeding the average increment per tree. The fact that there were only 18 individuals of ⩾ 20 m height in the plot in 1997 is testimony to the difficult conditions in this ridge crest plot, which not only has received repeated ash falls over the last 60 years, but is also subject to periodic drought stress (Whittaker *et al*. 1992*b*; c.f. Schmitt & Whittaker 1998).

### (c) *Panjang plot 1*

Plot P1 is dominated by *Dysoxylum*, which provided 46 out of 134 stems in 1989, declining to 43 out of 144 in 1992, and 36 out of 146 in 1997. The average mortality rate for the plot has increased only slightly during the period of ash deposition, from 2.5% $\mathrm{yr}^{-1}$ for 1989–1992, to 4.2% $\mathrm{yr}^{-1}$ for 1992–1997, with *Dysoxylum* experiencing about the plot average overall. Its relative decline in numbers is due to a lack of recruitment, with only two recruits in 1992 and none in 1997. Two species have increased significantly over the eight years, *Antidesma montanum*, from 26 to 46 individuals, and *Gnetum gnemon*, from 11 to 19 individuals. Both are relatively small trees at maturity. The substantial increase in standing biomass (figure 1) in this plot, is attributable to the continued growth of (and low mortality from) the canopy layer, which remains dominated by large *Dysoxylum*. This species provides 25 out of the 28 individuals of ⩾ 20 m height, the remaining three being *Neonauclea*.

While the above data suggest a relatively slight impact from volcanic effects in the 1992–1997 period, growth was slower than for 1989–1992, both in terms of dbh increment (table 2) and biomass ('growth' amounted to 37.2 Mg $\mathrm{ha}^{-1}$ for 1989–1992, and 32.4 Mg $\mathrm{ha}^{-1}$ for 1992–1997). Figure 2 shows that, as of 1997, *Dysoxylum* had a very unbalanced size structure in the plot, and the evident lack of recent recruitment would suggest an uncertain future. The number of species in the tree layer

Downloaded from rstb.royalsocietypublishing.org

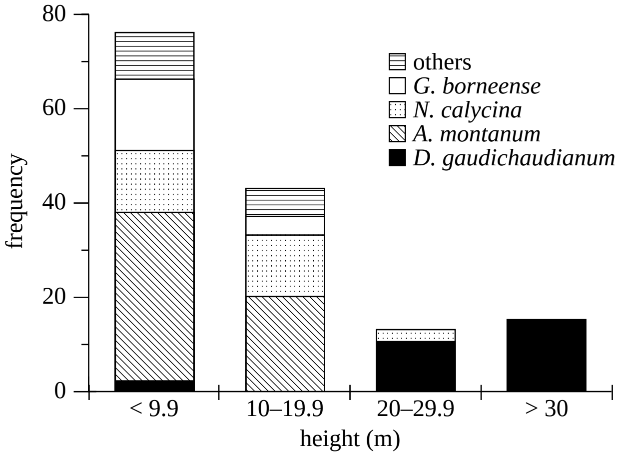

Figure 2. Tree height profile for plot Panjang 1 (P1) for 1997.

has varied from 15 in 1989, to 19 in 1992, to 13 in 1997, and from among the 13 there are relatively few species of stature similar to that of *Dysoxylum*. They include *Calophyllum inophyllum* (two individuals), *Buchanania arborescens* (one) and *Neonauclea* (29). *Dysoxylum* has shown a capacity to recruit into areas formerly occupied by *Neonauclea* in places in lowland Rakata (Schmitt 1997), and so it will be interesting to see what happens in this plot in the future. Most likely, the occurrence of *Neonauclea* as small trees in this plot indicates a past disturbance episode, as it appears to require high light levels and inorganic soils for establishment (Schmitt & Whittaker 1998). Given the paucity of alternative high canopy species, it may well be that *Dysoxylum* recruitment will follow once a few more of the larger canopy individuals of the species die and intraspecific competition between mature trees and saplings is reduced.

### (d) *Panjang plot 2*

Plot P2 is dominated by *Timonius*, which in 1989 had 94 out of 154 (61%) stems in the plot, but which declined to 86 out of 151 (57%) in 1992, and 66 out of 158 (41%) stems in 1997. While the plot average mortality rate increased only slightly from 3.03% $\mathrm{yr^{-1}}$ for 1989–1992, to 4.00% $\mathrm{yr^{-1}}$ for 1992–1997, the rate of loss of *Timonius* increased from 3.19 to 4.94% $\mathrm{yr^{-1}}$, with the average for all other species remaining constant at 2.77% $\mathrm{yr^{-1}}$ for both periods. Thus, once again, the dominant species of the plot has declined in numbers principally through a failure to recruit: in this case only one *Timonius* stem recruited during the eight years of the study. While in 1997 *Timonius* still provided 45 out of the 52 stems of $\geqslant 20$ m height, there were by contrast only three *Timonius* individuals of less than 10 m in height. Other species presently sharing the canopy include *Oncosperma tigillarium*, *Terminalia catappa*, *Buchanania arborescens*, *Neonauclea* and *Dysoxylum*, which in time may be added to by currently subcanopy individuals of *Ficus pubinervis* and *Calophyllum inophyllum*. Over the eight years, of the more abundant canopy species, *Oncosperma* (a multistemmed palm of modest height), increased from 21 to 33 stems, *Neonauclea* decreased from ten to nine stems, and *Dysoxylum* increased from seven to 18 individuals.

The plot began with a relatively high biomass, and even with the reduction from the 1992 peak, it remains at a high level. While the mean dbh increment was higher in the 1992–1997 period, the growth component of the change in biomass was reduced compared with the 1989–1992 period (tables 1 and 2). This is because of both the generally low growth of the mature, canopy-size *Timonius* and the attrition of this species from the canopy. Thus, the slight increase in rate of dbh increment in the second period came from the smaller trees. Over the eight years, the number of species in the plot increased from 11 in 1989, to 13 in 1992, to 17 in 1997. The data thus suggest a phase of successional change from a *Timonius*-dominated canopy, to a stand in which *Dysoxylum* looks likely to play an increasing role, but as part of a richer mix of canopy species than, for instance, is developing in the chronically disturbed plots on Sertung.

### (e) *Rakata plot 1*

Plot R1 is dominated by *Neonauclea*, which provided 49 out of 111 (44%) stems in 1989, 50 out of 124 (40%) in 1992, and 44 out of 128 (34%) in 1997. The plot average mortality rate for 1989–1992 was 3.3% $\mathrm{yr^{-1}}$, and for 1992–1997 it was 4.4% $\mathrm{yr^{-1}}$, with *Neonauclea* having lower rates than the average in each period (respectively 2.0 and 2.8% $\mathrm{yr^{-1}}$). The canopy remains dominated by *Neonauclea*, which provided 20 out of 33 trees of $\geqslant 20$ m height in 1997. Other canopy or potentially canopy-sized species in the plot in 1997 included *Ficus pubinervis* (23 individuals), *Radermachera glandulosa* (13 individuals), and *Dysoxylum*, *Buchanania arborescens*, *Ficus variegata* and *Terminalia catappa* (each less than five individuals). The most notable increase was in *Ficus pubinervis*, which increased from 11 to 23 individuals over the eight years. There has been considerable turnover of stems in the plot, without other major gains and losses: *Villebrunea rubescens*, a species of small stature, has shown the highest rate of turnover, with 11 out of the 12 individuals recorded in 1989 having failed by 1997, but with a correspondingly high number of new recruits to the plot, ending the period with 11 individuals. The number of species in the tree layer increased from 13 in 1989, to 16 in 1992 and 19 in 1997.

The apparent stability in biomass values for the plot (figure 1), thus hides a period of some dynamism. Several large gaps have developed within the plot over the study period, allowing relatively rapid growth (at least in dbh, c.f. table 2), quite pronounced turnover of some understorey elements, and a substantial increase in the representation of *Ficus pubinervis* in particular, at the expense of *Neonauclea*. In terms of the biomass contributed around 1997, these two species provide respectively 63 $\mathrm{Mg\,ha^{-1}}$ and 110 $\mathrm{Mg\,ha^{-1}}$ of the plot total of 229 $\mathrm{Mg\,ha^{-1}}$.

### (f) *Rakata plot 2*

Plot R2, the mid-altitude Rakata plot, was dominated in 1989 by *Neonauclea*, with 33 out of 107 stems. This fell to 29 out of 104 in 1992, 22 out of 77 in 1994 and 18 out of 110 in 1997, a reduction over the eight years from 31 to 16% of the stems in the plot. No recruits appeared in mitigation of the 15 losses of this species. It is still, however, the single most numerous species in the tree layer, and provides ten out of the 14 individuals $\geqslant 20$ m in height: the others being *Vernonia arborea* and *Villebrunea*

Downloaded from rstb.royalsocietypublishing.org

*rubescens*. The mortality rate for the plot was 3.74% $\mathrm{yr}^{-1}$ from 1989 to 1992, 18.75% $\mathrm{yr}^{-1}$ from 1992 to 1994, and 10.82% $\mathrm{yr}^{-1}$ from 1994 to 1997 (if calculated for the period 1992–1997, ignoring the 1994 survey, the rate would be 12.73%). The burst of high mortality began some time between August 1992 and July 1993, when lightning struck a group of trees, including an emergent *Ficus pubinervis* at the top of the plot. The fall of these large trees over the following two years led to the site unravelling, and a cascade of tree falls, undercutting and landslips (Whittaker *et al.* 1998). Much of the early ingrowth post-1992 has also subsequently been swept away.

The decline in biomass was abrupt, and was largely completed by 1994. As indicated in table 1, the period from 1994 to 1997, while still witnessing a high mortality of stems (with accompanying loss of biomass), has also been a period of rapid growth (the site mean dbh increment being 0.7367 cm $\mathrm{yr}^{-1}$), especially of subcanopy-sized trees. It has also been a period of rapid recruitment, with 58 individuals newly recruiting within just the three years. Interestingly, the number of species in the tree layer has increased from 12 to 17, with *Buchanania arborescens, Ficus ampelas, Macaranga tanarius, Omolanthus populneus* and *Pipturus argenteus* each recruiting into the gaps created within the plot. *Neonauclea* has been by far the biggest loser of this process, as it has failed to recruit, while the other larger trees in the plot, such as *Ficus pubinervis, Ficus tinctoria, Vernonia arborea* (the most numerous with 14 individuals) and *Radermachera glandulosa*, have more or less balanced losses with recruits.

### (g) *Rakata plot 3*

Plot R3, in the cloud forest at 680 m above sea level on Rakata, was dominated by *Saurauia* when first recorded in 1992. It then provided 82 out of 115 (71%) stems in the plot. Out of the 115, 43% had died by 1995 (Whittaker *et al.* 1998), and 59% by 1997. *Saurauia* lost 49 stems—in proportion to the plot average—over the five years, but recruited 26, to end the period with 59 stems out of a total of 97 (62%). The next most important species was *Vernonia arborea*, which had 14 stems in 1992, and which lost eight. Only two species gained in number over the five years. These were: *Ficus ribes*, which gained eight to end with ten individuals, and *Omolanthus populneus*, which gained eight to end with nine individuals. The canopy height in this plot is lower than in the lowlands, with no trees in excess of 19 m height. Stem diameters are also generally much lower than elsewhere. Hence, the biomass values for the plot are the lowest recorded (figure 1). Half of the standing biomass of 1992 had been lost by 1997, but this had already been nearly balanced by growth and by ingrowth (tables 1 and 2). Notwithstanding the tremendous turnover of individuals, the canopy remains dominated by *Saurauia*, with the above named species in support.

### (h) *Rakata plot 4*

Plot R4 was added to the programme in 1992, when *Neonauclea* provided 70 out of 100 stems in the plot. In 1997, it had declined to 57 out of 94 stems, losing 3.72% of its number per annum, a figure nearly identical to the plot average of 3.60% $\mathrm{yr}^{-1}$. Mortalities have been mostly of smaller stems, and none of the plot's 18 trees of greater than 30 cm dbh was lost over the five years. The canopy of the plot is formed largely by *Neonauclea* at around 25–32 m, with two large *Alstonia scholaris* and two large *Ficus pubinervis* forming an emergent layer at about 35 m height. The loss of biomass through mortality was the lowest of all the plots in the 1992–1997 period, and with no large canopy openings, there were also relatively few (12) recruits to the plot. The plot is in a mature phase, and consequently, when set up in 1992, had a high biomass value. This has increased further through the continued growth of the established trees (tables 1 and 2). The compositional balance of the plot has not changed much between 1992 and 1997, but the number of species in the tree layer did increase, from 15 to 18. This reflects the loss of *Morinda citrifolia* (one individual in 1992) and the recruitment to the plot of *Buchanania arborescens, Terminalia catappa, Litsea noronhae* and *Tarenna dasyphylla*, the latter two being small trees or shrubs hereby entering the permanent plots data set for the first time.

## 4. DISCUSSION

### (a) *Assumptions and limitations*

One obvious limitation of the use of permanent plots is that they cannot provide definitive answers to questions concerning events prior to their establishment. Thus, in respect to reconstructions of events from around 1934 up to 1979, a period for which very little information is available (Whittaker *et al.* 1989), the findings are necessarily of less direct value than they are for evaluating predictions made about future patterns of change. The permanent plots are each relatively small (figure 1), and so the results are subject to the idiosyncrasies of local patch dynamics, and may be misleading about general patterns of change across the islands. However, comparisons between the different plots should indicate which patterns are of general as opposed to local relevance.

The biomass estimates given here (figure 1, table 1) use an equation that has not been locally calibrated, and which is likely to overestimate when applied to Krakatau. Almost certainly the dominant species in each of the plots, being early-successional species, produce wood of lower density than is usual for mature forests in the region. Moreover, trees that have lost most of their branches through being damaged by the fall of other trees and the effects of volcanic ash deposition will clearly have a lower biomass for their trunk diameter and height than the equation predicts. Such trees feature particularly in the most heavily disturbed plots, and are probably more common within our data than in the forests from which the equations were developed. A further problem affecting estimates of growth increments, whether for dbh or biomass, is that some species have a tendency to develop buttresses. While bridging measurements were used in the study (c.f. Alder & Synott 1992), it is difficult to eliminate the effects of the early stages of buttressing from growth estimates. This problem occurs in larger individuals of *Dysoxylum gaudichaudianum*, and thus may have introduced error into estimates, particularly for plots S1 and P1. However, the data have been treated consistently within the study, and so the problems should be minimal when the data are used, as here, for comparisons within Krakatau (for comparisons with other sites, see Whittaker *et al.* (1998)).

Downloaded from rstb.royalsocietypublishing.org

### (b) *Evaluation of specific issues addressed in the paper*

#### (i) *Compositional change*

First, the 1997 data support previous findings of a reduction in *Neonauclea calycina* from the three Rakata plots in which it was dominant in 1989 (R1, R2 and R4 (1992)). This has occurred through a failure to recruit into the tree layer: only five recruits were recorded from plots R1, R2 and R4, and all of those were in plot R1. While *Neonauclea calycina* has also suffered mortalities, these have tended to be in proportion to the plot average. Although *Dysoxylum gaudichaudianum* has undoubtedly spread quite rapidly through parts of lowland Rakata (Schmitt 1997; Schmitt & Whittaker 1998), in the plots monitored, R1 and R4 muster between them only five individuals, and this species has yet to be recorded in the higher altitudes around R2. The data thus suggest that the decline in monodominance of *Neonauclea* is likely to correspond to the development of a more diverse set of stand types on Rakata (as suggested by Whittaker *et al.* 1989). Moreover, the size structures of each of the dominants in the plots on Sertung and Panjang similarly suggest the potential for significant compositional change (as illustrated for plot P1 in figure 2).

Second, the phase of increased volcanic activity has led to increased canopy turnover on Sertung (especially) and Panjang. It has also corresponded with increased disturbance through non-volcanic processes on Rakata, some of which may be linked to the volcano through increased storm activity centred on the group and through earth tremors and associated landslips (Schmitt & Whittaker 1998; Whittaker *et al.* 1998). While the plots that have been most disturbed have featured recruits of early successional species, e.g. *Macaranga tanarius, Ficus septica* and *Ficus fistulosa*, our expectation that *Timonius compressicaulis* would show a burst of recruitment has not been borne out within the plots. It has not recruited into plot S1, from which it was absent at the start of the programme, and in its plot of dominance on Sertung, S2, only one new individual and three additional stems have been recorded within the ingrowth. In plot P1, one individual recruited in 1992, but it died, leaving its representation at just two in the plot. Similarly, in plot P2, it has recruited only one stem since 1989. In this plot, where mature *Timonius* form the canopy, it has moreover suffered above the average rate of attrition for the plot, perhaps because the trees became overmature and less able to respond to physical stress. In plot S2, however, its survivorship has been above the average for the plot, indicating an ability to tolerate chronic disturbance as anticipated by Bush *et al.* (1992, for example p. 198). This plot has historically received greater thicknesses of ash from Anak Krakatau than any other in the programme (Whittaker *et al.* 1992*b*), and also appears to experience periodic water shortage in prolonged dry seasons (c.f. Schmitt & Whittaker 1998). The older *Timonius* trees typically show signs of having lost their lead growth points on more than one occasion, and many have developed a multiple-stemmed habit, suggesting a form of natural 'coppicing'. These fairly stunted trees have shown a capacity to survive despite spending lengthy periods caked in ash, and despite suffering significant loss of leaf cover.

Third, both *Timonius*-dominated plots (P2, S2) now provide some evidence of successful recruitment and growth of *Dysoxylum,* supporting previous suggestions (e.g. Whittaker *et al.* 1989) that the latter can grow through and dominate in such plots. In the chronically disturbed Sertung plot, S2, *Dysoxylum* appears to be virtually the only large tree species around to take over the plot, but in the less disturbed Panjang plot, P2, a somewhat more varied canopy is likely to develop.

#### (ii) *Changes in diversity*

Our expectation was that sites subject to chronic disturbance would feature depressed within-stand diversity, while elsewhere sites featuring 'normal' gap dynamic processes increased in diversity. While there are problems in defining what is meant by 'chronic', we are in no doubt that there was much more damage generally to the forests on Sertung from ash fall between 1992 and 1997 than there was on Panjang. Plot S2 declined from nine to seven species in the tree layer, while plot S1 held steady at 14, but with three losses (*Clerodendrum inerme, Ficus fulva* and *Terminalia catappa*) and three gains (*Buchanania arborescens, Bridelia monoica* and *Macaranga tanarius*). The Panjang plots showed an increase from 11 to 17 species in P2, and a decrease from 15 to 13 in P1. The three *Neonauclea*-dominated plots on Rakata each showed an increase in species in the tree layer, from 13 to 19 species in R1, from 12 to 17 in R2, and from 15 to 18 in R4. The summit plot, R3, showed a slight decline. Given that both R2 and R3 featured very high rates of stand turnover, and that R4 exhibited a low rate, it is difficult to draw clear conclusions from these data. However, it does seem likely that the chronic pollution on Sertung favours early successional species and makes it harder for new tree species to establish, and indeed the species entering our data set for the first time in 1997 were concentrated on Panjang (*Syzygium polyanthum*) and Rakata (*Tarenna dasyphylla* and *Litsea noronhae*). Moreover, while some patches of Rakata are undoubtedly subject to great disturbance, this has not involved chronic pollution from ash fall, which may thus continue to distinguish Rakata from Sertung and Panjang. The general attrition of *Neonauclea*-dominance on Rakata does seem to be linked to a continuing gradual diversification of the canopy.

#### (iii) *Growth responses and stand biomass*

Our expectation was that chronic disturbance would initially depress growth and standing biomass, but that this would be followed by rapid growth responses once the event has ended. There is a particular danger of circular reasoning in respect of this thesis, particularly so if we were simply to agree with it. However, the response of each plot has been in some respect distinctive, such that for instance, it does appear to fit events in the mid-altitude plot R2 on Rakata, but does not describe events in P1 on Panjang. In the latter plot, there was an increase in mortality during the period of ash fall from 1992 to 1997, and growth increments were reduced, but biomass continued to accrue in the stand, largely through the continued survivorship and growth of canopy-sized *Dysoxylum*. It is likely that the Panjang plots have not only experienced less ash fall than those on Sertung but that they have received less during the dry season, when it is much less likely to be washed from the foliage than

Downloaded from rstb.royalsocietypublishing.org

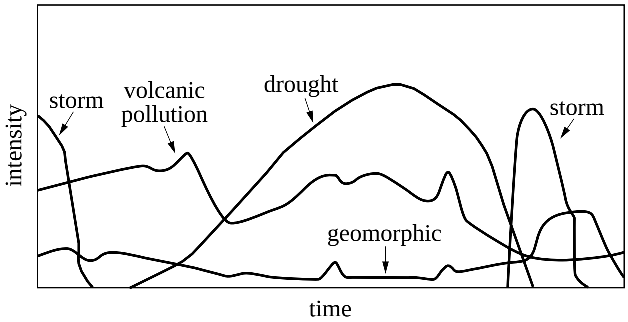

Figure 3. A trace of the varying temporal signals of differing (hypothetical) disturbance phenomena that may be influential on Krakatau. The impact on a stand of any particular disturbance event is likely to depend on the context, inclusive of the prior history of disturbance. Speed of onset, duration, timing in relation to phenological condition of the stand (dry versus wet season), physical characteristics of the event, and overlap in time and space with other disturbance phenomena, may each be important in influencing the ecological response.

during the wet season (Schmitt & Partomihardjo 1997). This may explain why the damage to the Panjang plots is evidently of a lesser degree than that on Sertung. Probably the greatest difficulty with evaluating this model, however, is that the ash fall events had only recently diminished prior to our survey in 1997, and so there had yet to be an opportunity for a clear response in terms of increased growth upon the 'ending' of the 'event'. Given the variety of values and trajectories for biomass of these stands (figure 1), it is not yet clear what the norms for stands on Krakatau may be, if indeed the notion of a normal stand volume is credible. Similar remarks might apply to growth increments, as rates clearly vary not only with stand density, but also as a function of, for example, intensity of the dry season (see Schmitt & Whittaker 1998).

### (c) *Concluding remarks*

Permanent plot studies may be established for a variety of purposes, including both silvicultural and ecological objectives (Alder & Synott 1992; Sheil 1995; Condit *et al.*, this issue; Newbery *et al.*, this issue). Depending on the objectives, they may involve proper experimental design, i.e. hypothesis formulation, treatments, controls, replicates and the use of inferential statistics. Or, at the other extreme, they may involve no formal initial hypotheses, no purposeful treatments, or replication, and they may most safely be analysed by descriptive statistics. The Krakatau permanent plot programme falls between these two extremes. The programme did have both general and specific goals. However, no purposeful treatments were carried out, the 'replication' within the design is imperfect, and what should constitute the control site(s) is unclear. The Rakata plots, which we thought would provide a 'baseline' against which to compare the impacts of volcanic disturbance on Sertung and Panjang, turned out to include two of the (so far) most disturbed plots within the programme. Forest ecological dynamics require longer than eight years for their understanding (e.g. see Crow 1980; Condit 1995; Sheil 1995; Condit *et al.* 1996), and several of the questions addressed in this paper can only be answered definitively at a much later stage of the programme. Nonetheless, the permanent plots programme has already enabled some questions to be answered.

Together with related studies of forest dynamic processes at the gap and landscape scales (Schmitt 1997; Schmitt & Partomihardjo 1997; Schmitt & Whittaker 1998), this project has been instrumental in a reassessment of the Krakatau forests. This has confirmed the importance of volcanic activity from Anak Krakatau, but has added to this an appreciation of the role of other episodic environmental disturbances in influencing stand dynamics and turnover. It should also be stressed, finally, that the impact of disturbance events is dependent upon their context (figure 3). One aspect is the timing of the initiation and ending of a disturbance episode in relation to the phenological rhythms of the forest, as this may determine which species of tree provide the seedlings to fill the space created (e.g. see Pascarella 1998). Another aspect is that the disturbances impact on an already varied vegetational mosaic and the effects of a disturbance episode (even on the same dominant species) will vary as a function of the previous history of the stand. The local availability of seed sources for particular species can also be crucial to the pattern of infill. While some species, such as *Macaranga tanarius*, have a good chance of being dispersed (in this case by birds) into virtually any large gap on the islands, other species have much more limited opportunities for rapid dispersal. An example of the latter type is *Semecarpus heterophylla*, which although also animal dispersed, produces a much larger seed and which so far remains highly concentrated in its distribution around two large parent trees in north-eastern Panjang (Schmitt & Whittaker 1998). It is the interaction of such patterns of differential species performance and availability, with site availability, environmental fluctuation and disturbance (c.f. Pickett *et al.* 1987), that produces much of the variation in successional pathways that has been demonstrated in this paper.

We are grateful to the Indonesian Institute of Science (LIPI), the Indonesian Directorate of Forestry and Nature Conservation (PHPA), and all those who helped record the plots from 1989 onwards, most especially Dr M. B. Bush and Dr S. F. Schmitt. We thank the ODA Forest Research Programme (Project R4739) for funding the 1992 survey, the Royal Society, the University of Oxford, Meyer International and Earthwatch Europe for financial or other support. This is Krakatau Research Project publication 56. This paper is based on material collected when R.J.W. was a participant in the Royal Society's South-East Asia Rain Forest Research Programme (Programme publication no. A/281).

## REFERENCES

Alder, D. & Synott, T. J. 1992 Permanent sample plot techniques for mixed tropical forest. *Tropical forestry papers*, no. 25. Oxford: Oxford Forestry Institute.

Backer, C. A. & Bakhuizen van den Brink, R. C. 1963–1968 *Flora of Java*. Three volumes. Groningen, The Netherlands: N. V. P. Noordhoff.

Brown, S. & Iverson, L. R. 1992 Biomass estimates for tropical forests. *World Res. Rev.* **4**, 366–384.

Bush, M. B. & Whittaker, R. J. 1991 Krakatau: colonization patterns and hierarchies. *J. Biogeogr.* **18**, 341–356.

Bush, M. B. & Whittaker, R. J. 1993 Non-equilibration in island theory of Krakatau. *J. Biogeogr.* **20**, 453–458.

Downloaded from rstb.royalsocietypublishing.org

Bush, M. B., Whittaker, R. J. & Partomihardjo, T. 1992 Forest development on Rakata, Panjang and Sertung: contemporary dynamics (1979–1989). *Geojournal* **28**, 185–199.

Bush, M. B., Whittaker, R. J. & Partomihardjo, T. 1995 Colonization and succession on Krakatau: an analysis of the guild of vining plants. *Biotropica* **27**, 355–372.

Compton, S. G., Ross, S. J. & Thornton, I. W. B. 1994 Pollinator limitation of fig tree reproduction on the island of Anak Krakatau (Indonesia). *Biotropica* **26**, 180–186.

Condit, R. 1995 Research in large, long-term tropical forest plots. *Trends Ecol. Evol.* **10**, 18–22.

Condit, R., Hubbell, S. P. & Foster, R. B. 1996 Changes in tree abundance in a neotropical forest: impact of climate change. *J. Trop. Ecol.* **12**, 231–256.

Crow, T. R. 1980 A rain forest chronicle: a 30-year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica* **12**, 42–55.

Docters van Leeuwen, W. M. 1936 Krakatau 1883–1933. *Annales du Jardin Botanique de Buitenzorg* **46–47**, 1–506.

Ernst, A. 1908 *The new flora of the volcanic island of Krakatau*. Cambridge University Press. (Translated into English by A. C. Seward.)

Gillespie, A. J. R., Brown, S. & Lugo, A. E. 1992 Tropical forest biomass estimation from truncated stand tables. *For. Ecol. Manage.* **48**, 69–87.

Lugo, A. E. & Scatena, F. N. 1996 Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* **28**, 585–599.

Nicholls, N. 1991 The El Niño/southern oscillation and Australian vegetation. *Vegetatio* **91**, 21–36.

Pascarella, J. B. 1998 Hurricane disturbance, plant–animal interactions, and the reproductive success of a tropical shrub. *Biotropica* **30**, 416–424.

Pickett, S. T. A., Collins, S. L. & Armesto, J. J. 1987 A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**, 109–114.

Schlesinger, W. H., Bruijnzeel, L. A., Bush, M. B., Klein, E. M., Mace, K. A., Raikes, J. A. & Whittaker, R. J. 1998 The biogeochemistry of phosphorous after the first century of soil development on Rakata Island, Krakatau, Indonesia. *Biogeochemistry* **40**, 37–55.

Schmitt, S. F. 1997 Disturbance and succession on the Krakatau Islands, Indonesia. DPhil thesis, University of Oxford, UK.

Schmitt, S. F. & Partomihardjo, T. 1997 Disturbance and its significance for forest succession and diversification on the Krakatau Islands, Indonesia. In *Plant diversity in Malesia III. Proceedings of the Third International Flora Malesiana Symposium 1995* (ed. J. Dransfield, M. J. E. Coode & D. A. Simpson), pp. 247–263. Kew, UK: Royal Botanic Gardens.

Schmitt, S. F. & Whittaker, R. J. 1998 Disturbance and succession on the Krakatau Islands, Indonesia. In *Dynamics of tropical communities*, British Ecological Society Symposium vol. 37, (ed. D. M. Newbery, H. N. T. Prins & N. D. Brown), pp. 515–548. Oxford, UK: Blackwell Science.

Sheil, D. 1995 A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. *For. Ecol. Manage.* **77**, 11–34.

Shilton, L. A., Altringham, J. D., Compton, S. G. & Whittaker, R. J. 1999 Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proc. R. Soc. Lond.* B **266**, 219–223.

Simkin, T. & Fiske, R. S. (eds) 1983 *Krakatau 1883: the volcanic eruption and its effects*. Washington, DC: Smithsonian Institution.

Tagawa, H. 1992 Primary succession and the effect of first arrivals on the subsequent development of forest types. *Geojournal* **28**, 175–183.

Tagawa, H., Suzuki, E., Partomihardjo, T. & Suriadarma, A. 1985 Vegetation and succession on the Krakatau Islands, Indonesia. *Vegetatio* **60**, 151–145.

Thornton, I. W. B. 1996 *Krakatau: the destruction and reassembly of an island ecosystem*. Cambridge, MA: Harvard University Press

Thornton, I. W. B., New, T. R., Zann, R. A. & Rawlinson, P. A. 1990 Colonization of the Krakatau islands by animals: a perspective from the 1980s. *Phil. Trans. R. Soc. Lond.* B **328**, 131–165.

Thornton, I. W. B., Zann, R. A. & Van Balen, S. 1993 Colonization of Rakata (Krakatau Islands) by non-migrant land birds from 1883 to 1992 and implications for the value of island equilibrium theory. *J. Biogeogr.* **20**, 441–452.

Thornton, I. W. B., Partomihardjo, T. & Yukuwa, J. 1994 Observation on the effects, up to July 1993, of the current eruptive episode of Anak Krakatau. *Global Ecol. Biogeogr. Letts* **4**, 88–94.

Walsh, R. P. D. 1996 Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *J. Trop. Ecol.* **12**, 385–407.

Whittaker, R. J. 1998 *Island biogeography: ecology, evolution and conservation*. Oxford University Press.

Whittaker, R. J. & Jones, S. H. 1994*a* The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *J. Biogeogr.* **21**, 689–702.

Whittaker, R. J. & Jones, S. H. 1994*b* Structure in rebuilding insular ecosystems: an empirically derived model. *Oikos* **69**, 524–530.

Whittaker, R. J., Bush, M. B. & Richards, K. 1989 Plant recolonization and vegetation succession on the Krakatau islands, Indonesia. *Ecol. Monogr.* **59**, 59–123.

Whittaker, R. J., Bush, M. B., Partomihardjo, T., Asquith, N. M. & Richards, K. 1992*a* Ecological aspects of plant colonisation of the Krakatau Islands. *Geojournal* **28**, 201–211.

Whittaker, R. J., Walden, J. & Hill, E. J. 1992*b* Post-1883 ash fall on Panjang and Sertung and its ecological impact. *Geojournal* **28**, 153–171.

Whittaker, R. J., Partomihardjo, T. & Riswan, S. 1995 Surface and buried seed banks from Krakatau, Indonesia: implications for the sterilization hypothesis. *Biotropica* **27**, 346–354.

Whittaker, R. J., Jones, S. H. & Partomihardjo, T. 1997 The rebuilding of an isolated rain forest assemblage: how disharmonic is the flora of Krakatau? *Biodivers. Conserv.* **6**, 1671–1696.

Whittaker, R. J., Schmitt, S. F., Jones, S. H., Partomihardjo, T. & Bush, M. B. 1998 Stand biomass and tree mortality from permanent forest plots on Krakatau, Indonesia, 1989–1995. *Biotropica* **30**, 519–529.

Downloaded from rstb.royalsocietypublishing.org