

# Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest

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## Summary

**1** The lowland rain forest at Pasoh Forest Reserve in Peninsular Malaysia is subject to disturbance by native wild pigs (*Sus scrofa*). Female pigs snap off woody plants up to 3.5 m tall to construct nests for reproduction, damaging >170 000 saplings km<sup>-2</sup> year<sup>-2</sup>. We investigated the ability of 1808 woody saplings to survive and resprout over a 3-year period following pig and experimental stem snap.

**2** Most plants resprouted to some degree, but, in understorey conditions, growth of new shoots was slow. More than 90% of stems were alive 3 months after damage, but > 40% had not yet produced a single fully expanded leaf. Mortality at 36 months was higher for resprouting saplings (33%) than for undamaged control saplings (9%). Survival of damaged stems was highly and positively correlated with stump basal diameter. Canopy species consistently showed lower survivorship than midstorey, understorey and treelet species but no differences in survivorship were found for habit (tree vs. liana) or leaf morphology (simple vs. compound).

**3** The number and total length of resprout shoots (TSL) were strongly, positively correlated with stump diameter. Canopy species produced greater TSL but fewer new shoots than did smaller-stature species. Trees and lianas produced similar TSL at 3 and 6 months, but trees produced more TSL at 12 and 36 months. Simple-leaved plants consistently had longer TSL than compound-leaved plants.

**4** Both species and families differed greatly in terms of survival, TSL and number of shoots. Dipterocarpaceae, which comprises 24% of basal area in the forest, and Euphorbiaceae, the most species-rich family, had especially poor survivorship of damaged individuals.

**5** Our results suggest that elevated pig densities found in small forest reserves such as Pasoh are likely to alter tree community composition as a result of the differential ability of species to regenerate following physical disturbance. Regeneration of canopy tree species, particularly in the silviculturally important and heavily dominant family Dipterocarpaceae, may be particularly susceptible to pig-related disturbance.

*Key-words:* Dipterocarp forest, nest building, Pasoh Forest Reserve, physical disturbance, *Sus scrofa*

*Journal of Ecology* (2003) **91**, 222–233

## Introduction

Woody plants are subjected to various types of physical disturbance that lead to loss of foliage or stems, and the relative ability of a species to resprout should be directly correlated with the frequency and intensity of disturbance. In tropical forests that are prone to large-scale disturbances such as hurricanes, plants of all sizes survive and resprout after being damaged (Walker 1991; Yih *et al.* 1991; Basnet 1993; Bellingham

*et al.* 1994). In tropical rain forests where large-scale disturbances are infrequent, understorey woody plants still experience significant stem damage from smaller scale disturbances such as branchfalls and treefalls (Aide 1987; Clark & Clark 1991). Consequently, the ability to resprout should be a common plant characteristic in these areas too. Although the frequency of branchfalls and treefalls is probably similar among lowland rain forest sites, additional causes of stem damage may be site specific. We investigated resprouting in understorey plants in lowland dipterocarp rain forest at Pasoh Forest Reserve (PFR) in Peninsular Malaysia, where nest building by native wild pigs (*Sus*

*scrofa*) is a common source of physical damage to saplings.

Pigs everywhere build nests to some degree, but the importance of this behaviour on understorey plant dynamics is higher at PFR than elsewhere within the range of *Sus scrofa* for two reasons. First, in other regions or habitats herbaceous plant material is often abundant and is used in nest construction with minimal impact on surrounding vegetation. However, there are few herbaceous plants in the understorey at PFR and consequently woody saplings are used in nest construction. Female pigs snap or uproot saplings 40–350 cm tall and gather the vegetation into a large mound under which they deliver their young. Plants that are uprooted entirely die, but stems that are snapped may resprout. Second, pig density has increased 10–100 times beyond historical levels at PFR (Ickes 2001b), due to the absence of large predators and an abundant year-round food supply in the agricultural areas that surround the 2500-ha forest reserve (Ickes & Williamson 2000). The number of nests constructed by pigs is therefore quite high (560 were constructed  $\text{km}^{-2} \text{year}^{-2}$  between 1996 and 1998) damaging an estimated 173000 saplings  $\text{km}^{-2} \text{year}^{-2}$ , of which 49% could potentially resprout (Ickes 2001a).

Studies of animal impacts on forest species composition and diversity have most commonly emphasized tree species' susceptibility to different sources of damage. For example, most herbivores in tropical forests are highly specific, feeding only on part of the total flora (Coley & Barone 1996; Barone 1998). In contrast, nest-building activities of pigs are more analogous to physical sources of disturbance because female pigs remove nearby individuals of all tree species within a selected size range. Thus, at Pasoh, woody species suffer in proportion to their abundance within the affected area. At the family level only two families differed in terms of susceptibility to pigs: members of the Dipterocarpaceae were taken more often, whereas stems from the Ebenaceae, all in the genus *Diospyros*, were used less often than would be expected based on abundance and proximity to the nesting site (Ickes 2001a). Although there is some clumping of nests within a given year, the areas in which nests are concentrated differed over several years such that pig nests were common throughout the study area (Ickes 2001a). Species may differ in their ability to resprout following physical disturbance as a consequence of differences in factors such as meristematic capacity, root-shoot partitioning, stored carbohydrate and nutrient reserves (Zimmerman *et al.* 1994).

To investigate resprouting of understorey plants, we followed for 36 months all stumps created by pigs in the construction of 10 nests as well as experimentally created stumps. We determined the overall proportion of saplings that resprouted following stem snap in this forest and asked whether (i) stump size influences resprouting, (ii) morphological and life history characteristics influence resprouting and (iii) there are differences in taxon-level survival or resprout vigour.

## Methods

### STUDY SYSTEM

Pasoh Forest Reserve is located 110 km south-east of Kuala Lumpur, Malay Peninsula ( $2^{\circ}59' \text{ N}$ ,  $102^{\circ}18' \text{ E}$ ). The reserve comprises a core area of 650 ha of primary lowland dipterocarp forest, an adjacent 650-ha buffer zone of regenerating forest selectively logged during 1956–59, and another 650–1000 ha of primary hill dipterocarp forest. A corridor of hill forest connects PFR to the southern end of the main mountain range of Peninsular Malaysia, but most of the perimeter (approximately 85%) abuts mature African oil palm (*Elaeis guineensis* Jacq.) tree plantations established in the 1970s. The flora of PFR is exceptionally diverse, with over 800 tree species  $\geq 1.0 \text{ cm d.b.h.}$  (diameter at breast height) recorded in a 50-ha plot (Kochummen 1997). Annual rainfall is approximately 2000 mm with a known range of 1700–3200 mm (Kochummen *et al.* 1990). Monthly rainfall means exceed 100 mm, but although the climate is technically aseasonal there may be consecutive months within a single year with substantially less than 100 mm of rain.

### STUMPS CREATED DURING NEST CONSTRUCTION

Ten new pig nests were located in the understorey away from gaps in the 50-ha tree plot. At each nest site all stumps created when a pig removed the upper portion of the stem for nest-building material were tagged, mapped and measured for basal diameter (hereafter BD) and height at the point of damage. BD was taken at the soil surface, or immediately above the basal swelling if one was present. Each nest was thought to be less than 48 h old at the time of discovery (10 June–5 November 1995), based on coloration and condition of the leaves in the nest and on the fresh condition of the surrounding stumps. Fresh stumps are easy to distinguish from older, dead stumps by their light-coloured, moist, clean wood at the top. Stumps were revisited at 3, 6, 12 and 36 months to determine mortality, species identification, number of shoots, shoot length, number of leaves per shoot and number of leaflets per shoot (for compound-leaved species). Total shoot length (hereafter TSL) was defined as the sum of the lengths of all resprout shoots, i.e. new growth excluding any branches below the point of stem snap that were present before damage occurred. With few exceptions, it was not possible to identify the species of stumps that did not develop resprout shoots. At each census, plants were recorded as dead if there were no leaves or shoots present and the wood was dry and brittle to the touch. If a stump appeared healthy but had no visible vegetative growth during one census but was dead by the next survey period, it was recorded as dead during the first survey.

To compare mortality of stem snapped vs. undamaged individuals, saplings that were not damaged

by pigs around each nest were tagged shortly after nest construction. Mortality was assessed for these plants at 36 months.

#### EXPERIMENTALLY CREATED STUMPS

We created experimental stumps that were identified before the stems were cut to determine whether there are species at PFR that do not resprout after stem snap damage. We established three 40 × 5 m transects approximately 500 m apart, divided them into eight 5 × 5 m plots, and measured and identified all trees ≥ 60 cm tall. In alternate plots all plants ≥ 60 cm tall and ≤ 2.5 cm d.b.h. were identified before cutting with a machete 20–60 cm above the ground. This size range is most likely to be used by pigs in nest construction, as pigs ignore smaller plants and cannot efficiently use larger ones. Plants in the other four plots were left uncut to serve as controls for comparing mortality at 36 months. Plants were censused in the same manner as were stumps created by pigs. Transects were parallel to, and 20 m inside, the edge of tall selectively logged forest that surrounds the core of primary forest in the reserve. The species in these transects are representative of primary forests as there is little change in light quality at the forest edge due to oil palm stems in the surrounding plantations (S. Thomas unpublished data).

In addition to measuring BD and stump height and noting the presence/absence of remaining leaves, we classified each stump according to four life history characteristics: habit (tree vs. liana), leaf morphology (simple vs. compound-leaves), stratum and abundance. Four 'strata' were recognized, based on each species' maximum d.b.h., derived from the census of the 50-ha plot at PFR (Manokaran *et al.* 1992), from the Tree Flora of Malaya (Whitmore 1972, 1973; Ng 1978; 1989), and from our knowledge of the flora. Species that seldom attain 2.0 cm d.b.h. were classified as 'treelets', those that regularly reach maximum d.b.h. 2–10 cm as 'understorey', 10–30 cm as 'midstorey' and > 30 cm as 'canopy'. A classification based on height could not be used because little information exists on maximum heights for tropical tree species. Lianas were excluded from all analyses where stratum was an independent variable. Monocots were included in the study but were uncommon (e.g. Arecaceae had only four individuals and Liliaceae had only nine individuals).

Four categories of abundance were employed based on a census of the 50-ha plot (Manokaran *et al.* 1992). Of approximately 340 000 stems, species with > 2000 stems were considered 'abundant' ( $n = 29$ ), species with 1000–2000 stems were 'common' ( $n = 42$ ), 500–1000 stems were 'uncommon' ( $n = 46$ ), and < 500 stems were 'rare' ( $n = 73$ ). It was not possible to obtain reliable information regarding the abundances of treelet species below the 1.0-cm d.b.h. threshold of the 50-ha plot. Data from other concurrent studies at PFR, however, provided information on 1959 individuals ≥ 70 cm tall and < 1.0 cm d.b.h. (e.g. Ickes *et al.* 2001),

and treelet species that had > 30 stems in this sample were considered abundant ( $n = 5$ ), 16–30 stems common ( $n = 6$ ), 6–15 stems uncommon ( $n = 7$ ), and < 6 stems rare ( $n = 9$ ). Lianas were again excluded from all analyses using abundance as the independent variable.

#### DATA ANALYSIS

SAS version 8.0 (SAS Institute 2000) was used for all statistical analyses. Bonferroni corrections to alpha (set originally at 0.05) were calculated for each subsection of the results to adjust for the number of tests. To determine if results from experimental and pig-created stumps were similar and could therefore be pooled, we first tested whether they had different likelihoods of resprouting and probabilities of survivorship. The effects on survivorship of continuous (BD and stump height) and ordinal categorical (abundance and strata) predictor variables were examined with logit models with a binomial random component. Effects of non-ordinal categorical predictor variables (habit and leaf morphology) on survivorship were analysed with loglinear models. Significance was evaluated with likelihood ratio chi-square tests of independence (PROC GENMOD, binomial distribution and logit link). We were unable to determine the habit, stratum or abundance for some individuals and thus had different sample sizes for each variable, so each effect on stump survival was analysed separately. For pig-damaged stems the species could not be determined unless and until it resprouted. As a result, it was impossible to test the importance of some variables on survivorship at 3 months. For example, we could only test if compound- and simple-leaved individuals survived pig damage to the same degree at 6, 12 and 36 months, but such analyses specifically test for differences in survival of individuals that *survived at least 3 months and resprouted to some degree*. However, as the vast majority of plants resprouted to some extent, the amount of information lost with those that died outright was minimal. Characteristics of resprouting individuals that survived to each time interval were examined by focusing on the length and number of shoots. Effects of non-ordinal categorical variables on TSL were examined using non-parametric analysis of variance (Kruskal–Wallis *H*-test). Continuous and ordinal categorical variables were correlated with TSL using Spearman rank correlations. Number of resprout shoots was examined using a Poisson regression for continuous variables and loglinear models for non-ordinal categorical variables (PROC GENMOD, Poisson distribution and log link). Individuals with no new shoot growth or number of shoots were excluded for analyses of TSL and number of shoots, respectively.

Differences in survivorship, TSL and number of shoots were also examined among species and families using data for the 13 species that had at least 16 identified stems. Survivorship was tested against con-specific, undamaged individuals found around the pig

necks and in the alternate  $5 \times 5$  m plots of the experimental stump transects, except for *Chasalia curviflora* (Rubiaceae) which could not be identified unambiguously until 36 months, by which time potential conspecific individuals may have already died. Survivorship differences between damaged individuals and undamaged plants were also compared between families.

Species identifications were determined in the field primarily by K. Ickes.

Reference collections were not made because leaf production on stumps was limited. Unidentified stems were removed from the data set for analyses that required species identifications (i.e. strata and abundance).

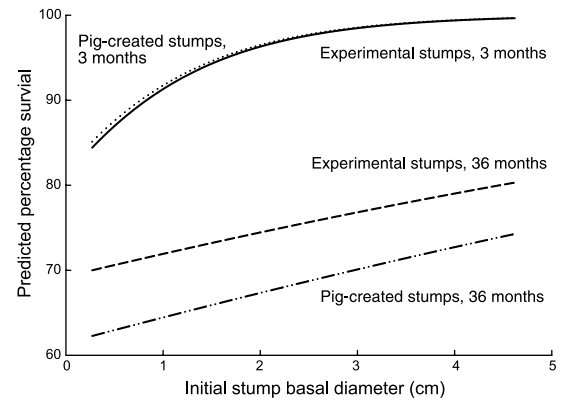
## Results

A total of 1808 stumps were examined for resprouting (1477 created by pigs and 331 created experimentally) of which 78% ( $n = 1405$ ) were identified to 257 species or morphospecies and 80% ( $n = 1445$ ) to family. The remaining 403 individuals could not be identified because they produced little or no foliage.

The ability to resprout to some degree was common among species found at PFR. At 3 months 75% of individuals had produced at least 2 cm of new growth, with an average shoot length of *c.* 15 cm. The rate of new leaf production, however, was not rapid. Fully 92.5% of the stumps were alive at 3 months but 15.4% had produced no new shoots and 41.5% had produced no fully expanded leaves. Virtually all plants (> 99%) that survived to 6 months produced some new shoot growth by this time, although 6.5% of these still had not produced a single fully expanded leaf.

*Pig-created vs. experimental stumps* – Both BD ( $\chi^2_1 = 26.5$ ,  $P < 0.0001$ ) and stump height ( $\chi^2_1 = 227.6$ ,  $P < 0.0001$ ) were significantly larger for experimental stumps, indicating that on average we cut larger saplings than pigs damaged, and that the experimental stumps were more comparable to the larger stems affected by pigs. The predicted percentage survival for pig and experimental stumps was similar across stump BD at 3, 6 and 12 months, but experimental stumps had higher survivorship at 36 months (Fig. 1). Pig and experimental stumps also did not differ in production of at least 2 cm of shoot growth by 3 months ( $\chi^2_1 = 0.6$ ,  $P = 0.42$ ) or a fully expanded leaf at 3 months ( $\chi^2_1 = 3.4$ ,  $P = 0.07$ ). Because size-dependent patterns in resprouting were similar between pig and experimental stumps (i.e. the type  $\times$  BD interaction was not significant for any time interval), all stumps were pooled for subsequent experimental analyses unless otherwise stated.

*Mortality* – Mortality after stem damage occurred at a somewhat constant rate over the 36-month study period (Fig. 2). At 36 months 67% of all stumps were alive, whereas 91% of undamaged saplings survived to this time period ( $\chi^2_1 = 387.3$ ,  $P < 0.0001$ ). When the experimental stumps were excluded, the survivorship



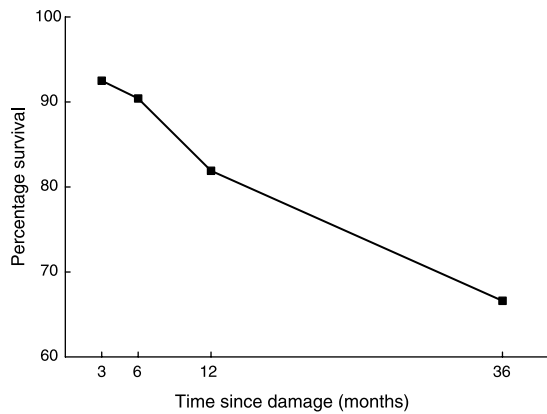
**Fig. 1** Predicted percentage survival in relation to initial basal diameter at 3 and 36 months post-damage at Pasoh Forest Reserve, Malaysia in relation to initial basal diameter. This relationship did not differ significantly between experimental and pig-created stumps at 3 months ( $\chi^2_1 = 0.05$ ,  $P = 0.82$ ), but experimental stumps had higher survivorship per initial basal area at 36 months ( $\chi^2_1 = 6.5$ ,  $P = 0.01$ ). Data for 6 and 12 months are not shown but were similar to the relationship at 3 months.

of pig-created stumps at 36 months dropped slightly to 65%. Survivorship data for undamaged saplings were not available at 3, 6 and 12 months.

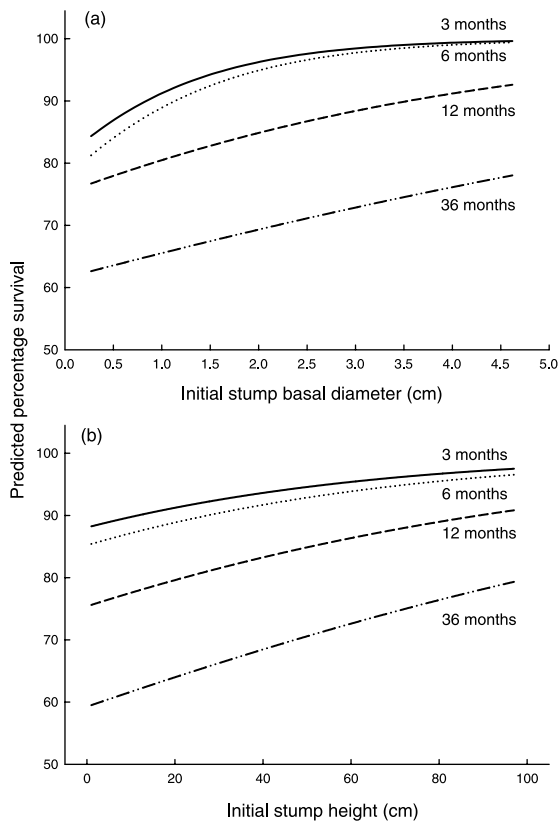
The initial physical characteristics of stumps strongly affected survivorship, particularly at early time intervals. Basal diameter was positively related to survivorship at 3, 6 and 12 months but the trend at 36 months was not significant (Fig. 3a). Stump height was also positively related to survivorship at all time intervals (Fig. 3b). However, stump height was positively correlated with stump BD (Spearman rank correlation  $r_s = 0.68$ ,  $n = 1374$ ,  $P < 0.0001$ ), and when both were considered in a logistic regression model, BD was a significant predictor of survivorship at 3 ( $\chi^2_1 = 15.6$ ,  $P < 0.0001$ ) and 6 ( $\chi^2_1 = 16.8$ ,  $P < 0.0001$ ) months but not at 12 and 36 months, whereas stump height was not a significant predictor of survivorship at any time interval. The presence of leaves below the point of damage did not affect survivorship at any time interval, though stumps with leaves were rare (only 4%,  $n = 68$ ). Thus, BD seems to be the most important of the measured characteristics for determining survival probabilities.

One natural history parameter was also a significant predictor: the stratum of adult trees was significantly related to survivorship of individual stems (Fig. 4a), with species from lower strata being more likely to be alive. Canopy species, in particular, had considerably lower survivorship than treelets, understorey, or midstorey species. Abundance was significantly related to survivorship only at 6 months and overall was not a strong predictor of stump survival (Fig. 4b). Neither growth habit (Fig. 4c) nor leaf morphology (Fig. 4d) was significantly related to survivorship at any time interval.

*Total shoot length (TSL)* – The summed length of all resprouting shoots on a given sapling (TSL) was used



**Fig. 2** Percentage survival of snapped stems over time at Pasoh Forest Reserve, Malaysia.



**Fig. 3** Survival of stumps vs. (a) initial basal diameter at 3 ( $\chi^2 = 19.3$ ,  $P < 0.0001$ ), 6 ( $\chi^2 = 21.7$ ,  $P < 0.0001$ ), 12 ( $\chi^2 = 6.0$ ,  $P = 0.01$ ) and 36 ( $\chi^2 = 3.1$ ,  $P = 0.08$ ) months, and (b) stump height at 3 ( $\chi^2 = 6.6$ ,  $P = 0.01$ ), 6 ( $\chi^2 = 7.5$ ,  $P = 0.006$ ), 12 ( $\chi^2 = 7.5$ ,  $P = 0.006$ ) and 36 ( $\chi^2 = 7.8$ ,  $P = 0.005$ ) months.

as an integrated measure of performance following disturbance. Average TSL increased over time since damage (mean  $\pm$  SE: 3 months  $17.9 \pm 1.0$  cm; 6 months  $24.6 \pm 1.2$ ; 12 months  $31.0 \pm 1.3$ ; 36 months  $55.4 \pm 2.7$ ). Stumps with larger initial BDs produced greater TSL at all four intervals, but with a weak correlation ( $r_s = 0.35$ – $0.50$ ;  $n = 1176$ – $1548$ ;  $P < 0.0001$  for all times). Taller stumps also produced greater TSL at

each time interval ( $r_s = 0.31$ – $0.46$ ;  $n = 1178$ – $1549$ ;  $P < 0.0001$  for all times), but stump height explained even less of the variation in TSL than did initial BD. Individuals with leaves that survived below the point of stem damage did not produce a different TSL from individuals that had all leaf area removed. Thus, BD seemed to be the major determinant of TSL production as well as of post-damage mortality.

Tree stratum affected TSL, with species from higher strata producing greater TSL at all time intervals (Fig. 5a). Average TSL did not differ with relative abundance at any time interval (Fig. 5b) and trees produced greater growth than lianes only at 36 months (Fig. 5c), but simple-leaved plants usually had higher TSL than those with compound leaves (Fig. 5d).

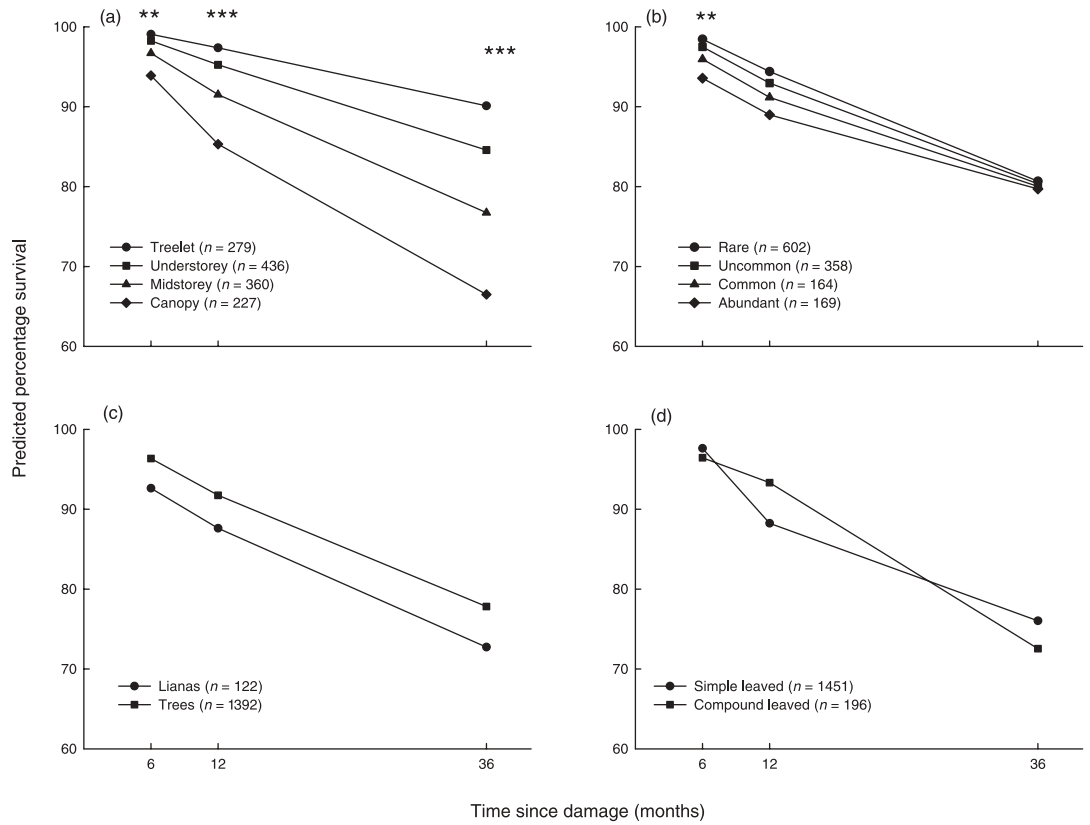
*Number of shoots* – Average number of new shoots did not change appreciably over time (3 months  $2.5 \pm 0.1$ ; 6 months  $2.7 \pm 0.1$ ; 12 months  $2.6 \pm 0.1$ ; 36 months  $2.4 \pm 0.1$ ). Stumps with greater initial BD produced more new shoots at all four time intervals (shown for 12 months in Fig. 6). The presence of leaves below the point of damage had no impact on the number of new shoots at any time interval.

The number of shoots produced was significantly different among strata; treelets had fewer shoots than larger strata at all times (Fig. 7a), mostly because at PFR treelets are often unbranched, and thus likely to produce only one new shoot after stem snap. Abundance was not related to number of shoots (Fig. 7b). Trees had more shoots than lianas at all times (Fig. 7c) and simple-leaved individuals always had more shoots than compound-leaved individuals (Fig. 7d).

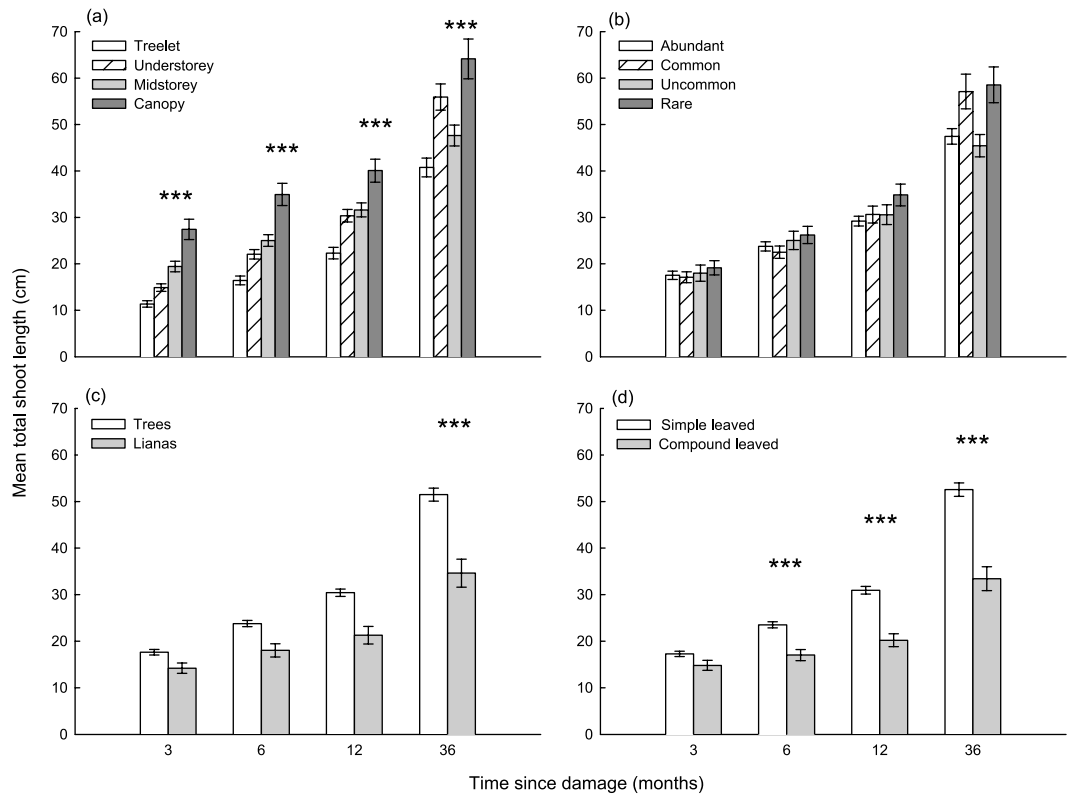
*Species-level responses* – The 13 most common species differed considerably in terms of survivorship, TSL, and number of new shoots (Table 1). There were overall significant differences in survivorship among the 12 species tested ( $\chi^2 = 63.61$ ,  $P < 0.0001$ ) and between damaged stems and undamaged conspecific individuals ( $\chi^2 = 43.04$ ,  $P < 0.0001$ ). *Shorea maxwelliana*, *Aporosa microstachya*, *Urophyllum hirsutum* and *Xerospermum norhanianum* had significantly lower survivorship than undamaged conspecifics (Table 1).

Species-specific differences were observed in terms of TSL at all time intervals: 3 months (Kruskal–Wallis  $H = 140.8$ ,  $P < 0.0001$ ), 6 months ( $H = 187.1$ ,  $P < 0.0001$ ), 12 months ( $H = 162.7$ ,  $P < 0.0001$ ), and 36 months ( $H = 139.3$ ,  $P < 0.0001$ ). *Urophyllum hirsutum* and *Rinorea anguifera* resprouted prolifically, whereas *Rinorea horneri* and *Lepisanthes tetraphylla* produced little TSL (Table 1).

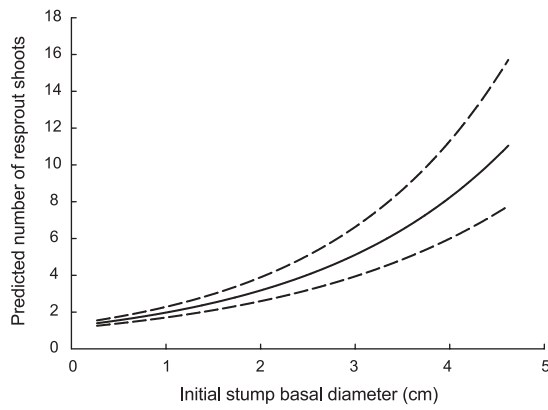
Number of shoots also differed among species at all time intervals: 3 months ( $\chi^2 = 217.9$ ,  $P < 0.0001$ ), 6 months ( $\chi^2 = 261.1$ ,  $P < 0.0001$ ), 12 months ( $\chi^2 = 215.2$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 143.8$ ,  $P < 0.0001$ ). On average, *Urophyllum hirsutum* produced 2–3 more branches than the other common species. The two compound-leaved species (*Lepisanthes tetraphylla* and *Xerospermum norhanianum*) both had  $\leq 1.5$  new shoots at 36 months (Table 1).



**Fig. 4** Survival of stumps for (a) stratum, (b) abundance, (c) habit and (d) leaf morphology over time since damage. \* $P < 0.003$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$  (Bonferroni adjusted). Total sample sizes differed slightly among life history characteristics because it was not possible to categorize all stems for all characteristics.



**Fig. 5** Mean total resprout shoot length per stump for (a) stratum, (b) abundance, (c) habit and (d) leaf morphology over time since damage. Bars represent  $\pm 1$  SE. Mean and SE values are based on a normal distribution. Spearman rank correlations were used to test the effects of stratum and abundance, and Kruskal–Wallis  $H$ -tests were used to test the effects of habit and leaf morphology. \* $P < 0.003$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$  (Bonferroni adjusted). Sample sizes as in Figure 4.



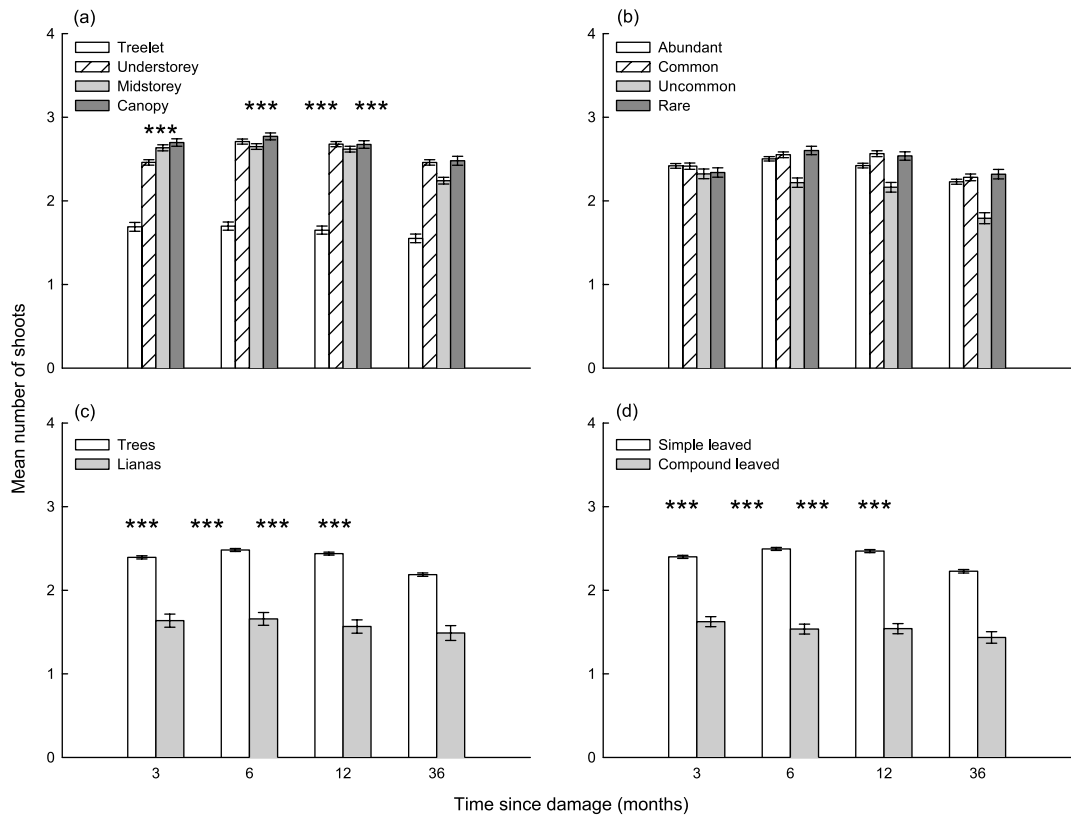
**Fig. 6** Predicted number of new shoots at 12 months based on stump basal diameter at time of stem damage based on a Poisson regression ( $\chi^2_1 = 239.5$ ,  $P < 0.0001$ ). Dotted lines represent the Wald 95% confidence interval. Estimates of shoot number at 3, 6 and 36 months gave similar curves.

*Family level responses* – Differences in resprouting were also found among the 19 families represented by 15 or more resprouting stems (Table 2). Among families overall, damaged individuals tended to have somewhat lower survivorship compared with undamaged individuals in the same family ( $\chi^2_{18} = 31.9$ ,  $P = 0.02$ ). Stumps from the Dipterocarpaceae had especially low survivorship.

Families differed in terms of mean TSL at 3 months ( $H = 166.2$ ,  $P < 0.0001$ ), 6 months ( $H = 174.1$ ,  $P < 0.0001$ ), 12 months ( $H = 152.5$ ,  $P < 0.0001$ ) and 36 months ( $H = 100.4$ ,  $P < 0.0001$ ). Myrtaceae and Polygalaceae produced the highest mean TSL of the 19 families considered, while Connaraceae and Sapindaceae produced the least at 36 months (Table 2).

Number of resprout shoots also differed at all time intervals (3 months  $\chi^2_{18} = 176.3$ ,  $P < 0.0001$ ; 6 months  $\chi^2_{18} = 227.7$ ,  $P < 0.0001$ ; 12 months  $\chi^2_{18} = 213.5$ ,  $P < 0.0001$ ; and 36 months  $\chi^2_{18} = 180.1$ ,  $P < 0.0001$ ). Melastomataceae, Myrtaceae, and Polygalaceae averaged  $> 3.5$  new shoots, whereas Connaraceae, Gnetaceae, Leguminosae, Myristicaceae, Sapindaceae and Sterculiaceae all averaged  $< 1.5$  new shoots at 36 months (Table 2).

*BD–d.b.h. regression* – Most studies of resprouting have examined larger trees and therefore used d.b.h., not BD, as the measurement of stem size. We were unable to measure d.b.h. because pigs snap stems below 1.3 m above ground. In order to compare our results with those from other studies, we regressed BD against d.b.h. for a sample of  $> 7000$  stems at PFR (data not shown). Basal diameter of 1.7 cm was equivalent to 1.0 cm d.b.h., and 3.0 cm BD corresponded to 2.0 cm d.b.h. (K. Ickes unpublished data). Consequently, 83% of stems in our study were  $< 1.0$  cm d.b.h. prior to damage and virtually all were  $< 2.5$  cm d.b.h.



**Fig. 7** Mean number of resprout shoots for (a) stratum, (b) abundance, (c) habit, and (d) leaf morphology over time since damage. Bars represent  $\pm 1$  SE of average count data. Poisson regression was used to test the effects of stratum and abundance, and loglinear models were used to test the effects of habit and leaf morphology. \* $P < 0.003$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$  (Bonferroni adjusted). Sample sizes as in Figure 4.

**Table 1** Percentage survival, mean total shoot length (TSL), and mean number of shoots at 36 months after stem damage for the 13 most common species resprouting after stem snap. All species are trees. For strata, T = treelet, U = understorey, M = midstorey, and C = canopy. All species are simple-leaved except for those in the Sapindaceae, which are compound. Survivorship between damaged and undamaged conspecific saplings was tested with likelihood ratio chi-square tests of independence

Species	Family	Strata	Percentage survival ( <i>n</i> )		<i>P</i>	TSL (cm)	No. of shoots
			Damaged	Undamaged		Mean ± SE ( <i>n</i> )	Mean ± SE
<i>Anaxagorea javanica</i> Bl.	Annonaceae	U	90.9 (44)	97.2 (106)		70.7 ± 9.8 (40)	3.3 ± 0.4
<i>Shorea maxwelliana</i> King	Dipterocarpaceae	C	60.2 (88)	81.6 (76)	*	66.1 ± 5.5 (51)	3.2 ± 0.2
<i>Aporosa microstachya</i> (Tul.) M.A.	Euphorbiaceae	U	73.2 (41)	100.0 (50)	**	44.7 ± 3.9 (29)	2.9 ± 0.2
<i>Ardisia crassa</i> C.B. Clarke	Myrsinaceae	U	73.3 (30)	91.7 (60)		33.9 ± 3.6 (22)	2.0 ± 0.2
<i>Ardisia species 2</i>	Myrsinaceae	T	75.0 (20)	81.8 (22)		57.4 ± 16.8 (15)	1.8 ± 0.2
<i>Chasalia curviflora</i> (Wall.) Thw.	Rubiaceae	T	–	–		50.4 ± 6.9 (23)	1.4 ± 0.1
<i>Rothmannia macrophylla</i> (R. Br. ex Hk. f.) Bremek.	Rubiaceae	T	96.6 (29)	95.2 (42)		35.1 ± 3.5 (28)	1.3 ± 0.1
<i>Urophyllum hirsutum</i> (Wight) Hk. f.	Rubiaceae	U	67.4 (43)	98.0 (49)	**	142.1 ± 18.2 (29)	5.1 ± 0.4
<i>Lepisanthes tetraphylla</i> (Vahl.) Radlk.	Sapindaceae	U	93.1 (29)	96.8 (31)		19.3 ± 2.0 (26)	1.2 ± 0.1
<i>Xerospermum norhanianum</i> Bl.	Sapindaceae	M	78.3 (60)	91.9 (124)		32.2 ± 3.2 (46)	1.5 ± 0.1
<i>Leptonychia glabra</i> Turcz.	Sterculiaceae	T	95.0 (20)	95.0 (20)		65.0 ± 7.4 (19)	1.5 ± 0.1
<i>Rinorea anguifera</i> (Lour.) O.K.	Violaceae	U	95.8 (24)	100.0 (30)		82.2 ± 10.8 (23)	3.4 ± 0.4
<i>Rinorea horneri</i> (Korth.) O.K.	Violaceae	T	89.7 (39)	92.1 (76)		24.7 ± 2.1 (34)	1.8 ± 0.1

*n* represents the number of individuals for the different variables. \**P* < 0.004, \*\**P* < 0.001 (Bonferroni adjusted).

**Table 2** Percentage survival, mean total shoot length (TSL) and mean number of shoots at 36 months after stem snap for the 19 families represented by at least 15 resprouting stumps. All stumps from Burseraceae, Connaraceae, Leguminosae and Sapindaceae had compound leaves whereas all other stumps were simple-leaved. T indicates that the family was represented in the study only by tree species; L indicates that the family was represented in the study only by liana species; and T/L indicates that both tree and liana stumps were recorded. No. of species shows how many species were represented in the damaged and undamaged categories for each family. The  $\chi^2$  tests for survivorship differences are conservative because only 79.9% of damaged stems could be identified to family whereas 96.4% of undamaged saplings were identified to family

Family	Habit	No. of species		Percentage survival ( <i>n</i> )		<i>P</i>	TSL (cm)	No. of shoots
		Damaged	Undamaged	Damaged	Undamaged		Mean ± SE ( <i>n</i> )	Mean ± SE
Annonaceae	T/L	22	22	86.6 (112)	95.6 (228)		58.4 ± 5.0 (94)	2.6 ± 0.2
Burseraceae	T	8	11	83.3 (18)	95.7 (46)		44.9 ± 11.4 (14)	2.0 ± 0.4
Clusiaceae	T	9	16	70.0 (30)	94.6 (55)	*	36.1 ± 5.8 (20)	2.3 ± 0.3
Connaraceae	L	4	5	93.3 (15)	97.6 (84)		24.7 ± 3.8 (14)	1.4 ± 0.2
Dipterocarpaceae	T	14	18	54.1 (157)	86.1 (215)	**	60.6 ± 4.3 (83)	2.8 ± 0.2
Ebenaceae	T	9	9	89.1 (46)	97.5 (81)		48.8 ± 4.9 (40)	1.7 ± 0.1
Euphorbiaceae	T	38	35	76.7 (210)	95.5 (381)	**	49.7 ± 3.2 (158)	2.6 ± 0.1
Gnetaceae	L	2	3	94.1 (17)	88.5 (26)		42.7 ± 3.6 (16)	1.1 ± 0.1
Leguminosae	T/L	9	18	89.0 (18)	89.8 (176)		42.7 ± 9.4 (16)	1.3 ± 0.1
Melastomataceae	T	3	8	76.5 (17)	96.9 (65)	*	60.8 ± 8.7 (13)	4.4 ± 0.9
Myristicaceae	T	7	8	76.0 (25)	100.0 (51)	*	34.8 ± 4.5 (19)	1.2 ± 0.1
Myrsinaceae	T	5	5	78.4 (74)	92.2 (128)		37.7 ± 4.8 (58)	1.7 ± 0.1
Myrtaceae	T	6	10	70.6 (17)	83.1 (71)		71.1 ± 12.3 (12)	4.1 ± 1.1
Polygalaceae	T	5	5	90.9 (22)	100.0 (32)		75.8 ± 10.5 (20)	3.6 ± 0.6
Rubiaceae	T	29	34	87.2 (243)	94.9 (466)	**	53.4 ± 3.9 (209)	2.0 ± 0.1
Sapindaceae	T	7	7	85.2 (101)	93.0 (185)		27.4 ± 2.0 (84)	1.4 ± 0.1
Sterculiaceae	T	5	3	85.7 (28)	97.6 (42)		56.6 ± 6.8 (24)	1.4 ± 0.1
Ulmaceae	T	2	3	68.4 (19)	100.0 (13)		49.0 ± 6.3 (13)	3.2 ± 0.6
Violaceae	T	3	3	92.9 (70)	94.1 (119)		48.9 ± 5.3 (65)	2.4 ± 0.2

*n* represents the number of individuals for the different variables. \**P* < 0.0026 and \*\**P* < 0.001 (Bonferroni adjusted).

## Discussion

Stem damage to woody plants is caused by a variety of sources, such as fires, hurricanes, wind throws, landslides and treefalls, which cause different types of damage.

The frequency and impact of these disturbances differs considerably among regions and ecosystems. Types of damage include partial or complete defoliation, bent or broken limbs, stem snap, tip up and complete loss of above-ground biomass (as may happen during a fire).

We limit our discussion of woody plant resprouting primarily to studies conducted in tropical or subtropical locations following stem damage caused by stem snap (i.e. partial or complete loss of foliage and severed main stem) because resprouting response differs as a function of abiotic conditions and the severity and type of damage (Bellingham & Sparrow 2000; Bond & Midgely 2001). The saplings in our study were primarily axillary rather than basal resprouters. Axillary resprouters are predicted to be more common in areas with lower and less intense frequency of disturbance than basal resprouters (Bellingham & Sparrow 2000).

Resprouting has been considered a significant component of plant life histories in many biomes, particularly in relation to levels of disturbance (Bellingham & Sparrow 2000; Del Tredici 2001), and seems particularly significant at PFR. It has been noted that almost all temperate angiosperm trees have the ability to resprout at least during the sapling stage of development (Del Tredici 2001), and resprouting may in fact be an ancestral trait in woody angiosperms (Wells 1969). However, community-wide resprouting ability tends to be more common in more humid forests and is higher in tropical sites than in temperate forests (Everham & Brokaw 1996). In the present study 89% of damaged individuals, representing more than 250 species, resprouted and were still alive at 6 months. This level of resprouting is remarkable given that most saplings damaged by pigs lost all photosynthetic area and that all stumps were located in low-light understorey conditions. Although the vast majority of stumps resprouted to some degree within 6 months, survivorship decreased through time: only 67% of all stumps and 65% of pig-created stumps survived to 36 months, compared with 91% of undamaged saplings. Nonetheless, percentage resprouting at PFR was higher than that reported for trees after stem snap in neotropical aseasonal rain forests: 27% in a Costa Rican cloud forest (Matelson *et al.* 1995), 41% in Amazonian Peru (Gorchov *et al.* 1993) and 51% in lowland Panama (Putz *et al.* 1983). No comparable data on resprouting following stem snap are available for the palaeotropics.

#### DOES STUMP SIZE INFLUENCE RESPROUTING?

At PFR there was a strong positive relationship between stump size and resprout success. This is in contrast to the pattern from Neotropical forest sites in which *smaller* rain forest trees had higher survivorship following stem snap (Putz & Brokaw 1989; Gorchov *et al.* 1993; Kammesheidt 1998; Paciorek *et al.* 2000). However, the range of DBHs in our study extended only to 2.5 cm, whereas for the neotropical studies 'small' trees often included any tree < 15 cm d.b.h. The primary source of stem snap in these forests is branchfalls and treefalls, which Clark & Clark (1991) have shown to be more likely to damage saplings 1–10 cm d.b.h. than either larger or smaller stems. This

pattern may select for a bell-shaped response of resprouting ability to d.b.h., whose peak may be masked by class sizes in the neotropical studies (e.g. 1–15 cm d.b.h. vs.  $\geq 15$  cm). Both neotropical data and the data from our study are consistent with resprouting success in rain forests not prone to large-scale disturbance being highest in stems 2.5–10 cm d.b.h. Among woody plants < 10 cm d.b.h., there may be a simple, positive stem-size–energy-reserve relationship such that larger saplings are more likely to survive stem damage due to greater amounts of accumulated energy reserves. Such a unimodal resprouting response to severe stem damage is consistent with the notion of an optimum size for storage reserves and has theoretical support (Iwasa & Kubo 1997).

Tropical forests that experience large-scale disturbance display different patterns in community-wide resprouting success to those reported here. In Jamaica, Puerto Rico and Nicaragua, 54–87% of trees of various size classes resprouted after hurricane-caused stem snap damage and there was no consistent relationship between stem size and resprouting (Boucher *et al.* 1990; Basnet 1993; Zimmerman *et al.* 1994; Bellingham *et al.* 1995). Because stem snap damage affects both small and large stems (from branchfalls and treefalls, and hurricane winds, respectively) it is not surprising that both small (< 15 cm d.b.h.) and large ( $\geq 15$  cm d.b.h.) trees resprout successfully.

#### DO MORPHOLOGICAL AND LIFE HISTORY CHARACTERISTICS INFLUENCE RESPROUTING?

Like other life-history traits, resprouting ability involves a trade-off. In this case, allocation to storage in roots or stems, which enhances resprouting ability and survival, involves a cost to growth or reproduction (Chapin *et al.* 1990; Iwasa & Kubo 1997; Kobe 1997). If stem-damaging disturbance is sufficiently frequent, differential ability to survive and resprout should influence the relative abundance of species in a given habitat (Knight 1975; Bellingham & Sparrow 2000). Correlative evidence from several studies has suggested that common tree species do in fact resprout more often than rare species in some forests (Basnet 1993; Matelson *et al.* 1995; Guariguata 1998), but other studies found no such relationship (Zimmerman *et al.* 1994; Bellingham *et al.* 1995). Our data from PFR also did not reveal a relationship between resprouting ability and abundance, nor were there consistent differences with regard to TSL produced or shoot number among abundance categories.

One mechanism to minimize the threat from falling debris is for individuals to increase in size as quickly as possible, such that the size stratum that a tree species ultimately attains may be correlated with resprouting. Tree saplings of 1–10 cm d.b.h. in Costa Rica experienced higher rates of stem damage from falling debris than either smaller or larger plants, and *within* the 1–10 cm

d.b.h. range the probability of stem damage was inversely correlated with stem size (Clark & Clark 1991). The same is true at PFR with regard to pig damage: plants that grow above 2.0 cm d.b.h. can essentially 'escape' the threat of stem snap by pigs, whereas treelet species always remain at risk as outlined by Guariguata (1998). At PFR, stumps of canopy species had significantly higher mortality than species occupying lower strata at all time intervals tested. Conversely, of plants that did survive to at least 6 months, canopy species produced significantly more TSL than species that occupy the lower strata. These data seem to support the 'escape' hypothesis and suggest that there may be different strategies for coping with potential stem damage. Smaller stature plants may store at least some reserves for resprouting, whereas trees of higher strata direct energy into height growth, thereby diminishing the risk of damage from falling debris and pigs. Saplings of smaller strata at PFR have higher wood densities, lower growth rates, and more shade-adapted photosynthetic physiology than larger stature trees (Thomas 1996; Thomas & Bazzaz 1999). These traits may help account for the greater resprouting capacity of smaller stature trees found here, although differences in root-shoot partitioning, and the capacity to store and remobilize carbohydrates, could also be critical.

We expected that simple-leaved species would have a greater capacity to resprout than compound-leaved species due to a lower investment in remobilized resources necessary to construct a single functional leaf. However, no significant difference in survivorship was detected between leaf morphologies. Stumps of compound-leaved species did have significantly lower TSL after 6 months and fewer shoots at all time intervals, but production of a rachis by compound-leaved plants may be functionally and energetically equivalent to production of longer TSL or an additional shoot. As we did not measure rachis length on compound-leaved species, differences in TSL and number of shoots between different leaf morphologies may not be represented clearly here.

We found no differences in mortality between tree and liana resprouts following stem damage, although trees did produce greater TSL at 12 and 36 months and more shoots at all time intervals. It is noteworthy that virtually all the stumps at PFR were in low-light, understory conditions. Liana species are generally light demanding (Schnitzer & Bongers 2002), thus an experiment investigating differential resprouting by growth habit at various light levels might yield different results.

#### ARE THERE DIFFERENCES IN TAXON-LEVEL SURVIVAL OR RESPROUT VIGOUR?

Differential resprouting ability among species has been shown in other studies (Bellingham *et al.* 1995; Guariguata 1998; Paciorek *et al.* 2000), and our data also demonstrated species differences in abilities to resprout following severe stem damage. Survivorship, TSL and shoot number varied considerably at the species level.

Some species- and family-level differences were explained by similarities in life history characteristics. However, in several cases even closely related species that share most or all life history characteristics showed considerable differences in resprouting. For example, stumps of the violaceous understory tree *Rinorea anguifera* and treelet *R. horneri* both had  $\geq 90\%$  survival, but *R. anguifera* averaged twice as many shoots and three times the TSL as the congener *R. horneri*.

Similar variation in resprouting responses was found among species in the Rubiaceae. The understory tree *Urophyllum hirsutum* had only 67% survival whereas the treelet *Rothmannia macrophylla* had 97% survival. Despite the overall poor survivorship of *Urophyllum*, however, stumps that did survive averaged almost 300% greater TSL at 36 months than either *Rothmannia* or *Chasalia curviflora*, another rubiaceaceous treelet. Similarly divergent resprouting responses were shown in shoot number and individual shoot length. *Chasalia* and *Rothmannia* produced on average  $< 1.4$  shoots per stump at 36 months. In both species, when two or more branches were present, one was often the leader and comprised the majority of TSL while other shoots were short ( $< 5.0$  cm), perhaps held in reserve. In contrast, *Urophyllum* averaged 5.1 shoots per stump at 36 months, and most of the shoots continued to grow, so a single stump could have 10 shoots  $> 15$  cm in length at 36 months. The proliferation of sprouts following damage in *Urophyllum* may allow this species and others to take advantage of increased light levels following gap formation or removal of understory competitors.

Survivorship, mean TSL and mean shoot number also varied considerably at the family level. Dipterocarpaceae and Euphorbiaceae had especially poor stump survivorship. The low resprouting ability in the Dipterocarpaceae is notable because it is the most important timber family in the region, accounting for  $> 24\%$  of the basal area and 9 of the 10 most common emergent tree species at PFR (Kochummen 1997). The poor performance of Euphorbiaceae is also significant because it is the most species-rich family throughout Asian aseasonal lowland forests (Soepadmo 1995); 87 Euphorbiaceae species are present in the 50-ha plot at PFR, composing 11% of total tree species richness (Kochummen *et al.* 1990). Interestingly, Euphorbiaceae had the lowest survivorship of resprouts among all tree families in a lowland rain forest of Panama (Paciorek *et al.* 2000), suggesting that relatively poor resprouting ability may be characteristic of this family.

#### PIGS AND POTENTIAL CHANGES IN PLANT COMPOSITION

As *Sus scrofa* is native to Peninsular Malaysia, nest building has probably been a source of stem damage to understory plants for thousands of years in this area.

However, pig density is currently extremely high at PFR, probably having increased an order of magnitude in recent decades (Ickes 2001b) due to the lack of feline predators, which can not survive in such a small reserve or are removed as dangerous when they move outside the forest, and to year-round food supply in the surrounding African oil palm plantations. Pig density estimates were 27–47 individuals km<sup>-2</sup> from 1996 to 1998, and during this interval 560 pig nests km<sup>-2</sup> year<sup>-1</sup> were constructed, damaging > 170 000 stems km<sup>-2</sup> year<sup>-1</sup>. Approximately 50% of damaged stems were uprooted and killed, while 50% were snapped and may subsequently resprout (Ickes 2001a). Clearly, pig-caused damage to the understorey vegetation is a significant source of stem snap.

The physical disturbance in the understorey of PFR caused by nest building may substantially alter tree species composition in future generations because pigs snap saplings without regard to species (Ickes 2001a), but there is considerable variation in the ability of species to survive and resprout. We found no relationship between current levels of abundance and the ability to resprout, but the PFR flora may be 'out of equilibrium' with the current pig-disturbance regime (cf. Bellingham & Sparrow 2000). Indeed, models of resprouting and disturbance frequency predict that selection of life history strategies that include resprouting should increase with increasing levels of disturbance (Bellingham & Sparrow 2000). A shift away from the currently dominant Dipterocarpaceae and Euphorbiaceae, toward a subset of prolifically resprouting taxa, perhaps understorey treelets and shrubs, might be expected. PFR may be an extreme case of increased animal-related damage resulting from increases in animal densities within reserves, but shifts in community composition following animal-induced damage to vegetation have been proposed in several studies, e.g. elephant browsing in African savannahs (Barnes *et al.* 1994) and white-tailed deer browsing in eastern North America (Long & Carson 1998). We concur with Guariguata (1998) that 'interspecific patterns of post-damage response' may generally be a critical life-history parameter that affects the structure, species composition and diversity of tropical forests. Differential resprouting ability may become increasingly important in determining patterns of regeneration and species composition as tropical forests become increasingly fragmented and human–forest interfaces become more extensive.

### Acknowledgements

We are grateful for the field assistance of Kate Walker, Brian Funk, Scott Ickes, Rob Tizard and Alison Styring. G. Bruce Williamson, David Burslem, Doug Boucher and one anonymous referee made helpful suggestions to the manuscript while Chris Paciorek helped with regressions. K.I. and S.J.D. were funded in part by Board of Regent's Fellowships from Louisiana State

University. K.I. also received funding from the Center for Tropical Forest Science and Grants-in-Aid of Research from the National Academy of Sciences through Sigma Xi. S.C.T. was funded by the National Science Foundation, USA. We thank Dr Abdul Razak, Director General of the Forestry Research Institute Malaysia (FRIM), for permission to conduct research at Pasoh Forest Reserve. The 50-ha tree plot at Pasoh is part of the Center for Tropical Forest Science, a global network of large-scale demographic tree plots. The Pasoh 50-ha plot has been generously funded by FRIM and the National Science Foundation, USA.

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Received 1 July 2002

revision accepted 4 December 2002