

THE EFFECTS OF WILD PIGS (*SUS SCROFA*) ON WOODY UNDERSTORY  
VEGETATION IN LOWLAND RAIN FOREST OF MALAYSIA

A Dissertation

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy

in

The Department of Biological Sciences

by

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B.A. Swarthmore College, 1992  
December 2001

This dissertation is dedicated with love to my parents, Roy and Judi Ickes.

## ACKNOWLEDGMENTS

As with any sizeable endeavor in a person's life, successfully completing a dissertation would not be possible without the support of more than a few good people. Such generous support and personal interactions not only makes the achieving of one's goals feasible, but also makes the endeavor itself an enjoyable, worthwhile experience in and of itself.

G. Bruce Williamson has been a model graduate student advisor throughout my tenure at Louisiana State University. At various times, and whenever required, Bruce provided logistical support, his time, advice, trust, space to make my own decisions, encouragement, direction, and friendship. My committee members, Barry Moser, Kam-biu Liu, and Mark Hafner, all kindly gave of their time to review and make critical comments on each manuscript and dissertation chapter.

I am grateful to the Forestry Research Institute of Malaysia (FRIM) in general, and to the Director General, Dr. Razak, in particular, for permission to work at Pasoh Forest Reserve. FRIM, along with the Center for Tropical Forest Science, generously granted me access to the data set of a large, permanent tree plot located in Malaysia. While working in Malaysia, the success of my efforts depended greatly on the assistance, both professional and personal, of S. Appanah and Samad bin Latif. Developing friendships with these two men was one of the highlights of my time in Southeast Asia.

Also in Malaysia, various people contributed their time and energy by helping me to conduct fieldwork. First and foremost, Sean Thomas provided critical advice and assistance during the first six months of fieldwork, and subsequently made helpful comments to every manuscript and chapter. Roy Ickes, Judi Ickes, Scott Ickes, Saara DeWalt, Brian Funk, Alison Styring, Kate Walker, Rose McCauley, Tristram Seidler, and Rob Tizard all provided invaluable assistance and friendship in the field.

Chris Paciorek of Carnegie Mellon University provided statistical expertise for analysis of data in Chapter II. He will be a co-author on the manuscript when it is published.

Finally, I am uniquely grateful to Saara DeWalt for her support and companionship over the past four years. She made it pleasurable, and quite simply, possible.

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## ABSTRACT

An increasingly urgent task in the field of conservation biology is to identify changes in abiotic and biotic interactions that result when large areas of forest are converted to small fragments surrounded by anthropogenic landscapes. My research, conducted in lowland dipterocarp rain forest at the 2,500-ha Pasoh Forest Reserve in Peninsular Malaysia, investigated a novel but strongly negative edge effect - namely, a tremendous increase in the density of wild pigs (*Sus scrofa*) and the resulting deleterious impacts on the understory plant community. The absence of feline predators due to the small size of the reserve and the presence of a year-round food supply in the agricultural areas surrounding the reserve are believed to be the main factors contributing to increased pig density.

Line transects were conducted to determine pig density within Pasoh. Density in 1996 and 1998 was estimated to be 47 and 27 pigs/km<sup>2</sup>, respectively, or 10 – 100 times historical levels. Fences were constructed to exclude pigs from control plots to quantify the impact of soil rooting and seed predation on plants in the understory. After two years, plots inside exclosures had three times more recruits, greater species richness, and 53% more height growth among plants 1 – 7 m tall than did adjacent plots to which pigs had access. Surveys were conducted in 1995, 1996, and 1998 to determine the number of reproductive nests constructed by pigs. Pigs constructed an estimated 6.0 nests/ha/year during this time, with an average nest composed of 145 snapped saplings and 117 uprooted saplings. Nest building accounted for 28.9% of all mortality for trees 1 – 2 cm diameter at breast height. Uprooted stems died, but snapped stems produced a leafless stump that could resprout. Observations of >1,800 stumps for 36 months revealed large differences in resprouting among species, families, and groups of plants with similar life history characteristics. Overall, the results of the different studies suggest that if elevated pig densities continue there could be a shift away from the currently dominant Dipterocarpaceae and Euphorbiaceae.

## INTRODUCTION

Mammals interact with and influence individual plants or plant communities through a variety of behaviors: foraging, browsing, burrowing, digging, dam and nest building, seed predation, and trampling. Such behaviors have been shown to influence plant population and community dynamics or alter plant composition and diversity in a wide variety of habitats. In all cases of plant-animal interactions, animal density plays an important role in the extent to which plants and plant communities are affected.

As forests continue to be logged and many areas converted to agricultural use, the remaining fragments of forest undergo changes in biotic and abiotic conditions called edge effects. While some mammal species, such as large carnivores, often disappear from smaller patches of forest, other species may undergo a sharp increase in local density in response to the disappearance of natural predators or to altered conditions in the anthropogenic lands surrounding the forest fragment. In some cases, the now comparatively abundant species have been shown to have strong, deleterious impacts on the forest plant community. For example, logging, forest fragmentation, and fencing in some parts of Africa forces elephants (*Loxodonta africana*) to concentrate foraging in small forest remnants or reserves. Consequently, the overall number of elephants is low at the regional scale, but increased locally. High elephant density has resulted in increased tree damage and mortality, forest degradation, and retarded forest succession (Jachmann & Croes 1991; Struhsaker 1997). In another example, extensive logging outside park boundaries of Gunung Palung National Park in Borneo has caused changes in the foraging behavior and possibly migratory patterns of bearded pigs (*Sus barbatus*), which specialize on the fruit and seed crops of supra-annual mast fruiting episodes (Curran & Leighton 2000). The quantity of mast produced in secondary forests was drastically reduced compared to unlogged forests, forcing pigs to concentrate their feeding during masting periods in the primary forest inside the park boundary, substantially increasing local pig density. The dominant tree family in the 150,000-ha national park, Dipterocarpaceae, showed a complete lack of seedling recruitment over a 10-year period due to the intense seed predation by bearded pigs (Curran *et al.* 1999).

For my dissertation I sought to investigate the previously undocumented edge effects potentially caused by the hyper-abundance of wild pigs (*Sus scrofa*) on understory plants in primary lowland rain forest at Pasoh Forest Reserve, Peninsular Malaysia. I chose to focus on two aspects of pig behavior, nest building and soil rooting, which appeared to be especially disruptive to understory plants.

It was necessary to quantify pig density in the reserve in order to interpret pig-plant interactions in an ecologically meaningful way. Was the damage to plants from pig nest building and rooting that I documented in Chapters II - IV part of the normal process of plant-animal interactions in Malaysian rain forests? Or was pig density unusually high within the reserve, possibly due to extinction of natural predators and a potential year-round food supply from the agricultural lands adjacent to the reserve? I used line-transects to document pig density in 1996 and 1998 and compared the results with density estimates from other regions and habitats (Chapter I).

When delivering young, female pigs seek shelter under thick shrubs or gather vegetation into a pile and crawl underneath to give birth. In primary lowland rain forest of Malaysia, however, understory plants are not densely branched due to the low light

conditions and herbaceous ground cover is scarce. Instead, pigs use tree and liana saplings up to 3.5 meters in height to construct nests, either uprooting the plants entirely or snapping their stems. The resulting nest is a large, dome-shaped pile of vegetation composed of up to 500 woody plants. Many of the understory plants immediately surrounding pig nests are damaged or killed in the process. I investigated various aspects of nest building and how the understory vegetation is impacted. Some of the issues I addressed are how many pig nests were constructed per year, the number and size of plants used to construct nests, what species were used, and how nest building impacted annual tree mortality rates (Chapter II).

Approximately half the saplings used in nest construction by pigs were uprooted and killed outright, but the rest were snapped with only the top portion taken, leaving behind a 20 – 60 cm tall stump that may resprout. As more than 50,000 stumps/km<sup>2</sup>/year were created by pigs at Pasoh Forest Reserve, resprouting saplings may play an important role in the future composition of this forest. I investigated the ability of woody plants to resprout by following 1,800 stumps for 36 months, relating various physical and life history characteristics to successful resprouting (Chapter III).

A large proportion of a pig's diet is subterranean in origin and the animals regularly root through soil (Genov 1981; Singer 1981). Rooting may affect vegetation directly by displacing and killing seedlings or indirectly by altering physical properties of the soil, changing nutrient dynamics (Lacki & Lancia 1983; Singer *et al.* 1984), or facilitating the spread of exotic vegetation (Aplet *et al.* 1991). I quantified the impact of soil rooting on the understory by constructing fences to exclude pigs. After two years I compared the vegetation from these experimental plots with control plots outside fences to which pigs had access (Chapter IV).

No research has been conducted in Southeast Asia on any aspect of the biology of wild pigs, including pig-plant interactions. Pasoh Forest Reserve is only 2,500 hectares, and smaller reserves often require more active management than larger ones due to more pronounced edge effects. It was my goal to investigate the previously undocumented edge effect involving unusually high pig density and concomitant increases in soil rooting and number of reproductive nests constructed in this forest reserve. My hope is that the information provided by these studies will assist the Forestry Research Institute of Malaysia and the Malaysian Wildlife Department in the decision making process with regard to the active management of this and other small reserves.

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## CHAPTER I.

### HYPER-ABUNDANCE OF NATIVE WILD PIGS (*SUS SCROFA*) IN A LOWLAND DIPTEROCARP RAIN FOREST OF PENINSULAR MALAYSIA

This chapter is in press in *Biotropica*.

## INTRODUCTION

Vertebrate frugivores, granivores, grazers, and browsers play important roles in plant species population and ecosystem dynamics by acting as agents of seed dispersal (Schupp 1993; Mack 1998), seed predation (Becker & Wong 1985; Blate *et al.* 1998; Curran & Webb 2000), herbivory (Crawley 1983; Johnston & Naiman 1990), and physical disturbance (Holcroft & Herrero 1984; Whicker & Detling 1988). Particularly when the relative or absolute densities of vertebrates fluctuate to unusually high levels, the impact on individual plant species or ecosystems may be profound. For example, elephants (*Loxodonta africana*) in parts of Africa and bearded pigs (*Sus barbatus*) in Borneo have increased in density at a local scale because logging, forest fragmentation, or fencing have forced them to concentrate foraging in smaller areas. High local elephant density has resulted in increased tree damage and mortality, forest degradation, and retarded forest succession (Struhsaker 1997; Tafangeyasha 1997). In a Bornean national park the dominant tree family, Dipterocarpaceae, showed a complete lack of seedling recruitment over a 10-year period due to intense seed predation by pigs (Curran *et al.* 1999). Because medium to large-bodied vertebrates can have such profound impacts on surrounding environments there is a need for information on their densities as habitats are modified anthropogenetically. Habitat fragmentation and top-level predator removal may lead to local increases in density for some species, which in turn may provoke faster changes in ecosystem processes. Addressing such negative interactions is likely to be an ongoing challenge facing conservation biologists in our increasingly fragmented landscape.

Another example of elevated population densities of a terrestrial mammal is the wild pig (*Sus scrofa*). In its native range at Pasoh Forest Reserve (PFR) in Peninsular Malaysia, the wild pig population is thought to have increased considerably in recent decades and consequently to have had negative impacts on plants and animals. Soil rooting by pigs is thought to facilitate the spread of an exotic plant into the primary forest (Laurance 2000; Peters 2001) and to have reduced the local density of small terrestrial mammals (Kemper & Bell 1985). A pig exclosure study at PFR showed that after only two years woody seedling recruitment, stem density, and species richness increased inside exclosures compared with control plots to which pigs had access (Ickes *et al.* 2001). In addition to soil rooting, female pigs build large reproductive nests out of up to 500 uprooted or snapped off woody saplings that may be 2.5 cm diameter at breast height and 3.5 meters tall. Liu *et al.* (1999) modeled the effects of nest building by pigs within PFR and estimated that even moderate densities of pigs and the subsequent damage to trees would likely result in lowered tree species richness.

Despite the documented and hypothesized negative effects of pigs on plants and animals in Peninsular Malaysia, there are no estimates of pig density. I present evidence that the current density at PFR is extremely high in comparison with other sites where *Sus scrofa* occurs naturally. It is impossible to know if the high density reported here is typical of the region because these data represent the first estimates of pig density from the highly diverse aseasonal rainforests of Southeast Asia. I suggest, however, that pig density at PFR is much higher than historical levels in this forest type, and that the increase is due to an absence of feline predators and a year-round food supply from tree-plantations that surround the reserve.

## MATERIALS AND METHODS

### Study site

Pasoh Forest Reserve (PFR) is located in the state of Negeri Sembilan, 110 km southeast of Kuala Lumpur, Malay Peninsula (2° 59' N, 102° 18' E). The reserve comprises three areas: a 650-ha core of primary lowland dipterocarp forest, a 650-ha buffer zone of lowland forest selectively logged almost 50 years ago, and another 650 – 1,000-ha of primary hill forest. Aside from a narrow corridor of hill forest that connects PFR to the southern end of the main mountain range, the remaining perimeter (approximately 85%) abuts mature African oil palm (*Elaeis guineensis* Jacq.) plantations. Annual rainfall is approximately 2,000 mm with a known range of 1700 – 3200 (Kochummen *et al.* 1990). Monthly rainfall means exceed 100 mm, resulting in an aseasonal climate.

A number of herbivorous/frugivorous terrestrial mammals no longer occur at PFR, which may influence the population dynamics of *Sus scrofa* through lack of competition. Locally extinct species include Indian elephant (*Elephas maximus*), Javan rhinoceros (*Rhinoceros sondaicus*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), and gaur (*Bos gaurus*) (Medway 1983; Kemper 1988; Kochummen 1997). Other potential competitors of wild pigs that may still be present in the reserve at extremely low densities include the Malayan tapir (*Tapirus indicus*), sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*), greater mouse-deer (*Tragulus napu*), and bearded pig (*Sus barbatus*). The leopard (*Panthera pardus*) and tiger (*Panthera tigris*), the primary natural predators of wild pigs, have been rare or absent in the area since the 1960's. Hunting is not allowed within the borders of PFR, but poaching is not uncommon and legal hunting occurs at the boundaries of the reserve.

### Line transects

To minimize the amount of clearing required to conduct this study, only trails already established previously in the reserve were used as line transects. Ideally, line transects should be established randomly throughout the habitat being surveyed (Buckland *et al.* 1993). This is seldom possible in forest reserves, however, because of limitations on how many trails may be cut and where they can be placed. As a consequence, it was not possible to survey the hill dipterocarp forest in the northeast portion of the reserve (Fig. 1.1). Therefore, the resulting density estimates apply only to the flat, fairly homogenous habitat that comprises the rest of the reserve. All transects were located in primary forest except transect #1, which was located in the selectively logged forest (Fig. 1.1).

Line transect surveys were conducted during two separate periods: 5 May – 10 October 1996, and 17 May – 28 October 1998. The 13 transects were 500 - 1,600 meters in length and each was walked 5 – 10 times over the course of the study period. Total transect length of 12,880 meters in 1996 was reduced to 12,495 m in 1998 due to treefalls that caused two transects to be shortened. Transects were walked on foot at an approximate rate of 1 km / hr, primarily by K. Ickes, but occasionally a second observer was present or conducted a survey alone. To standardize for time, all transects were completed within the first 3 hours or the last 2.5 hours of daylight. On days when surveys were conducted, one or two transects were walked in the morning and one or two at night, though the same transect was never walked twice in one day. An attempt was made to

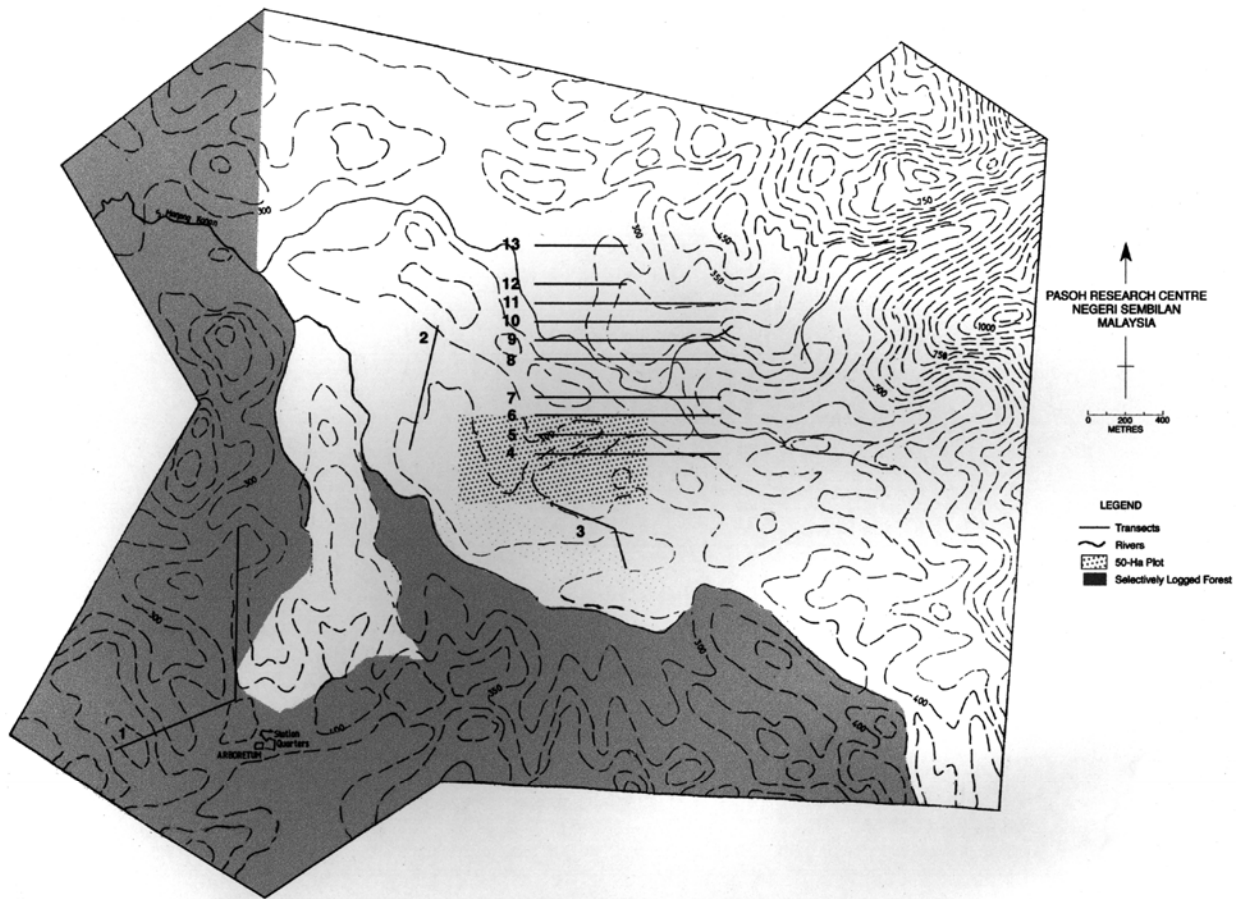


Figure 1.1 Topographic map of Pasoh Forest Reserve, Peninsular Malaysia (modified from a map provided by the Forestry Research Institute Malaysia). Contour lines are 50-ft increments. The 13 transects are numbered along which searches were conducted for *Sus scrofa* in 1996 and 1998.

walk all transects an equal number of times over the course of the study, but in two cases transects had to be temporarily abandoned due to nests of a king cobra and an aggressive wasp species. When it was difficult to detect pigs due to darkness or rain, a measurement of how much of the transect had been completed to that point was taken and the survey stopped. For example, if 400 meters of a 1,000 m transect had been completed when a storm developed, any observations (or lack thereof) to that point were recorded and the length of that transect was recorded as 400 m for that day. Transects 4 – 13 had been established previously as part of an ornithological study plot, which was used by researchers in July 1996 (Fig. 1.1). In that month, no pig surveys were conducted on those transects. Outside of the ornithological study, the transects were used minimally or not at all by researchers.

When a solitary pig was encountered, the animal was observed until it moved away. The perpendicular distance from the trail to the point where the pig was first observed was measured to the nearest meter using a tape measure. The time of observation, location along the transect, size of animal, and sex (when possible) were also recorded. Careful notice was taken of the direction in which the animal moved to minimize recording the same individual later on that transect. When multiple solitary individuals were seen on the same transect, in all but one case it could be reliably determined that they were separate individuals due to differences in size, sex, or the direction of movement of the prior individual. In the one case when it was not possible to make such a decision clearly, the second observation was discarded. When a group of pigs was encountered, perpendicular distance was measured to the center of the group. Groups were followed when possible to obtain better counts of individual numbers.

Two age classes of pigs were recognized. “Young” pigs have a distinctive striped appearance consisting of yellow-brown longitudinal bands separated by black, a pattern retained for up to four months (Eisenberg & Lockhart 1972; Diong 1973). Large pigs possessing uniform coloration were considered “adult”. Because pigs become reproductive around 6 – 8 months in age (Diong 1973), all pigs considered “young” would have been pre-reproductive individuals, whereas some of the “adult” pigs were probably pre-reproductive but most were likely of reproductive age.

To compare the density of pigs at PFR with other studies, estimates were obtained from the literature for locations and habitats within the native range of *S. scrofa*. These estimates were obtained by various methods, differing in precision. Nonetheless, all prior density estimates encountered in the literature were listed here if the methodology used to generate the estimate was moderately rigorous. Reports in languages other than English were not listed if an adequate translation of methodology could not be obtained.

### **Data analysis**

Density estimates were generated using the program Distance version 3.5 (Thomas *et al.* 1998). Calculations of mean group size included solitary sightings as a group size of one.

Biomass estimates of *S. scrofa* were calculated using two average weights, one for young and one for adults. The proportion of the total estimated density with uniformly gray coloration was multiplied by 62.0 kg, a mean weight value used elsewhere (Dinerstein 1980). No estimates of weights of young *S. scrofa* in Southeast Asia could be

found in the literature, thus an arbitrary weight of 10.0 kg was used to calculate biomass of young individuals (see results).

## RESULTS

During the 1996 survey, 88 transects were walked for a total of 81.0 km. There were 44 pig sightings: 25 solitary individuals and 19 groups with two or more individuals (see Fig. 1.2 for group size distributions; Fig. 1.3 for sighting distance from the trail). Mean group size was 3.8 individuals. The largest group of pigs encountered comprised 32 animals: 6 large adults and 26 striped young. Overall, 166 pigs were seen, including 73 striped young. A half-normal/cosine detection function was used to generate a density estimate of 47.0 pigs / km<sup>2</sup> with a 95% confidence interval of 28.2 – 78.6 pigs / km<sup>2</sup> and a coefficient of variation of 26.4%. Biomass of *S. scrofa* was estimated to be 1,837 kg / km<sup>2</sup>.

A similar search effort was made during the survey in 1998, when 91 transects were walked for a total of 79.9 km. The 1998 survey yielded 39 sightings: 19 solitary individuals and 20 groups with two or more individuals (Fig. 1.2, Fig. 1.3). The largest group encountered in 1998 comprised 10 animals: 4 adults and 6 striped young. Mean group size was 3.3 individuals. In total, 129 pigs were seen, of which 30 were striped young. The half-normal/cosine detection function estimated pig density in 1998 to be 27.0 pigs / km<sup>2</sup> with a 95% confidence interval of 16.2 – 44.7 pigs / km<sup>2</sup> and a coefficient of variation of 26.0%. Biomass was estimated to be 1,346 kg / km<sup>2</sup>.

Determining the sex of individual pigs was not always possible. When sexual determinations could be made, adult males were usually seen as solitary individuals. Adult females were often observed in same sex groups with or without young, or in groups of one adult female with young.

Within the native range of *S. scrofa*, few studies estimated population densities greater than 5– 10 individuals / km<sup>2</sup> (Table 1.1). On Peucang Island off the west coast of Java, an island too small to maintain predator populations of pigs, Pauwels (1980) estimated a density of 27 – 32 individuals / km<sup>2</sup>. The highest estimates of *S. scrofa* within its native range were from two sugarcane fields in Pakistan. One 3,327-ha sugarcane field had 32.2 pigs / km<sup>2</sup>, and a 2,037-ha field had 72.1 pigs / km<sup>2</sup>. No natural predators occurred in these agricultural areas, and the pigs fed voraciously on the cane, destroying up to 35% of the crop before being removed with poison (Shafi & Khokhar 1985).

## DISCUSSION

This study, conducted in lowland equatorial rain forest within the native range of *S. scrofa*, estimated that densities at Pasoh Forest Reserve were 47.0 and 27.0 individuals / km<sup>2</sup> in 1996 and 1998, respectively. There are three possible interpretations of these high estimates of pig density for this aseasonal rain forest in Malaysia. First, the data may over- or under-estimate pig densities at this site. Without additional, independent estimates this possibility cannot be excluded. However, line transects are recognized as one of the most practical and reliable methods for estimating densities of larger mammals in most habitats (Buckland *et al.* 1993; Mandujano & Gallina 1995; Varman & Sukumar 1995). Furthermore, pigs were reported to be common in the reserve in the mid 1980's

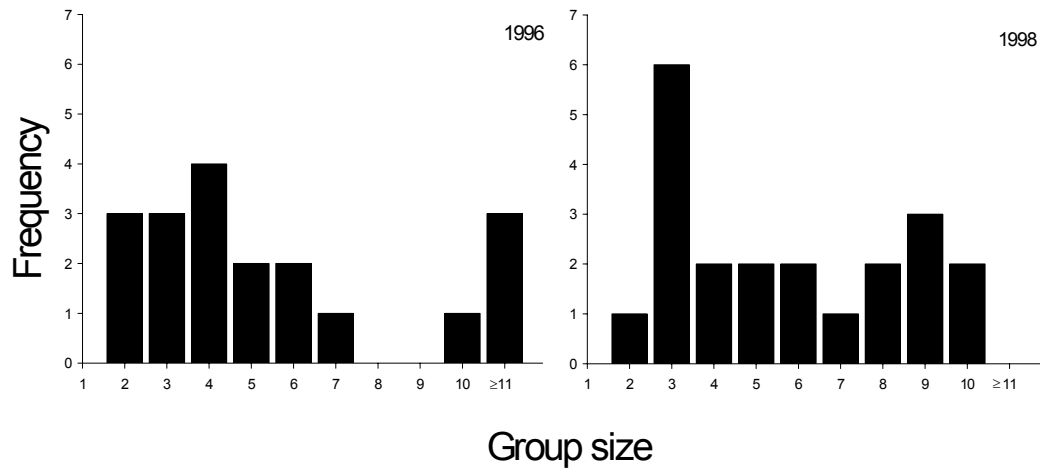


Figure 1.2 Number of pigs in all group sightings (i.e. sightings of two or more individuals) for the line transect surveys conducted at Pasoh Forest Reserve, Malaysia, in 1996 and 1998. The three groups of > 11 pigs in 1996 had 16, 23, and 36 individuals. In 1996 and 1998, the number of solitary pig sightings was 25 and 19, respectively.

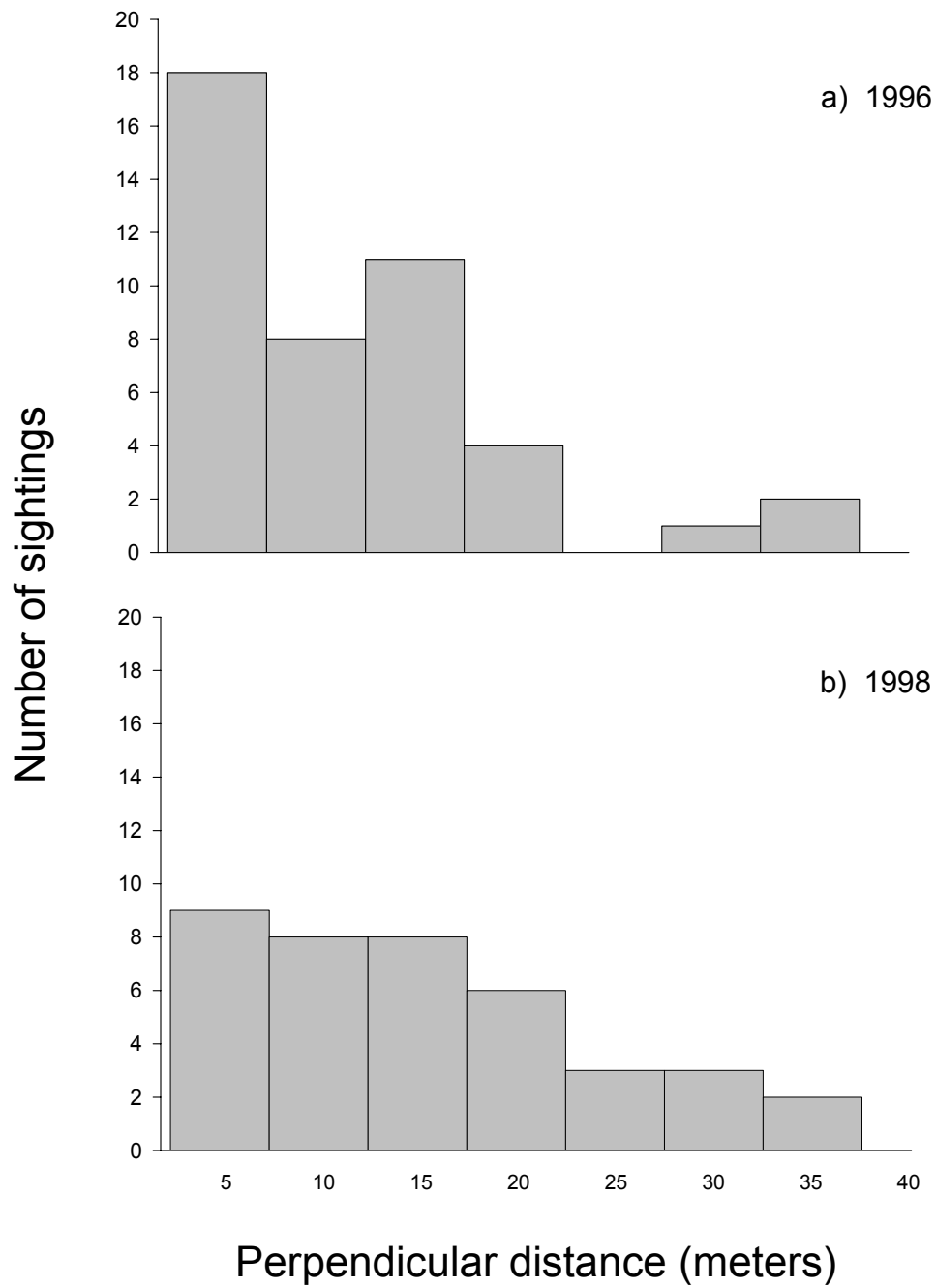


Figure 1.3 Number of pig sightings at 5m increments perpendicular to the trail in (a) 1996 and (b) 1998 at Pasoh Forest Reserve, Peninsular Malaysia.

Table 1.1 Density estimates of *Sus scrofa* within its native range. Locations are organized by country in alphabetical order. Data from Pash Forest Reserve are shown in bold face.

Country	Location	Vegetation type	N / km <sup>2</sup>	Source
Assam	Kaziranga Wildlife Sanctuary	Riparian forest, grassland	1.3 - 1.5	Spillett (1967a)
India	Keoladeo Ghana Sanctuary	Grassland, marsh	2.9	Spillett (1967b)
India	Jaldapara Wildlife Sanctuary	Riparian forest, grassland	1.2 - 1.4	Spillett (1967c)
India	Nagarahole National Park	Tropical moist deciduous and dry deciduous forest	4.2	Karanth and Sunquist 1992
India	Gir Forest, Gujarat	Tropical dry deciduous forest	0.1	Berwick and Jordan 1971
India	Gir Forest, Gujarat	Tropical dry deciduous forest	< 1.0	Khan et al. 1996
India	Kanha National Park	Tropical dry deciduous forest, Sal forest, grassland	1.2	Schaller 1967
Indonesia	Peucang Island, Ujung Kulong Nat Park	Coastal, disturbed, and dipterocarp forest; swamp	27 - 32	Pauwels 1980
Italy	Maremma Natural Park	Mediterranean	5.1 - 6.1	Massei and Tonini 1992
<b>Malaysia</b>	<b>Pash Forest Reserve 1996</b>	<b>Lowland dipterocarp rain forest</b>	<b>47.0</b>	<b>This study</b>
<b>Malaysia</b>	<b>Pash Forest Reserve 1998</b>	<b>Lowland dipterocarp rain forest</b>	<b>27.0</b>	<b>This study</b>
Malaysia	Dindings district, Perak	Dipterocarp and coastal forest, agriculture	< 1.0	Diong 1973
Nepal	Royal Chitwan National Park, Java	Riverine forest, tall grassland	5.8	Seidensticker 1976
Nepal	Royal Karnali-Bardia Wildlife Reserve	Sal, riverine, and hardwood forests; grassland	4.2	Dinerstein 1980
Nepal	Royal Karnali-Bardia Wildlife Reserve	Savannah, grassland	3.8	Dinerstein 1980
Pakistan	Chiniot, Sargodha District	Sugarcane fields	32 and 72	Shafi and Khokhar 1985
Pakistan	Changa Manga Forest, West Pakistan	Irrigated forest plantation	10.4	Inayatullah 1973
Pakistan	Thatta District, Southern Pakistan	Riparian forest, agricultural fields, swamp	3.7	Smiet et al. 1979
Poland	Various locations	Deciduous forest / agriculture	1.2 - 1.8	Mackin 1970
Poland	Augustow Forest	Coniferous forest	0.3 - 2.0	Pucek et al. 1975
Poland	Pszczyna Forest	Coniferous forest	1.0	Pucek et al. 1975
Poland	Niepolomice Forest	Coniferous forest	0.2	Pucek et al. 1975
Poland	Smolniki Forest	Coniferous forest	1.0	Pucek et al. 1975
Poland	Zielonka Forest	Coniferous forest	1.6	Pucek et al. 1975
Poland	Bialoweiza Forest	Deciduous forest	2.0	Pucek et al. 1975
Poland	Niepolomice Forest	Deciduous forest	0.4	Pucek et al. 1975
Poland	Zielonka Forest	Deciduous forest	3.1	Pucek et al. 1975
Sri Lanka	Ruhuna National Park	Lowland monsoon forest, savanna woodland, grassland	0.7	Santiapillai and Chambers 1980
Sri Lanka	Wilpattu National Park	Lowland monsoon and monsoon scrub forest	0.3 - 1.2	Eisenberg and Lockhart 1972
Sri Lanka	Gal Oya National Park	Lowland monsoon forest, savanna woodland, grassland	0.6	McKay 1973
Thailand	Huai Kha Khaeng Wildlife Santuary	Several dry forest habitats	< 0.5	Srikosamatara 1993

(Kemper 1988), and that pigs are still extremely common is obvious from the amount of soil area rooted daily and the frequency of sightings (pers. obs.).

A second interpretation for these data is that they accurately represent the situation at PFR and that *S. scrofa* naturally occurs at these densities in aseasonal dipterocarp rainforests of Southeast Asia. Data from two other studies from Malaysia, however, suggest that the densities reported here for PFR are much higher than elsewhere in the Peninsula. Diong (1973) investigated *S. scrofa* in the northern state of Perak and estimated the total pig population of the “Dindings district” to be only 800 animals. Although Diong did not state how large of an area this covered, based on his map it appears that *S. scrofa* density in the area was well below 1.0 / km<sup>2</sup>. Laidlaw (1994) walked line transects in seven different Virgin Jungle Reserves in Peninsular Malaysia (PFR not among them) and averaged only one sighting (group or solitary individual) of *S. scrofa* for every 14.0 km surveyed. Encounter rates were much greater in this study at PFR: in 1996 *S. scrofa* was encountered once every 1.8 km surveyed, and in 1998 once every 2.1 km surveyed. If it is assumed that the average group size was comparable between studies, the density of pigs at PFR was approximately seven times higher than at the Virgin Jungle Reserves. Taken together, the results of Diong (1973) and Laidlaw (1994) suggest that density estimates of 47 and 27 pigs / km<sup>2</sup> reported here for Pasoh Forest Reserve do not accurately reflect typical *S. scrofa* densities in lowland aseasonal dipterocarp forest.

The third, and most probable, interpretation for these high pig densities is that they accurately represent the current situation at PFR, and there have been changes in and around the reserve in recent decades that have contributed to a dramatic increase in pig density. Two such changes that may have been especially important in allowing pig density to rise and be maintained at such high levels in this forest are the local extinction of the natural predators of wild pigs and the presence of African oil palm tree plantations surrounding the reserve (Ickes & Williamson 2000).

In various locations and habitats within the native range of *S. scrofa*, where native large predators and *S. scrofa* still co-occur, pigs are a principal food item in the diets of several carnivorous species (Eisenberg & Lockhart 1972; Rabinowitz 1989; Karanth & Sunquist 1995). Within the aseasonal dipterocarp forests of Peninsular Malaysia and Sumatra, pigs are probably a major prey item for both tigers and leopards, particularly since there are fewer potential Cervid prey species in this habitat compared with the more open, seasonal forests elsewhere in Southeast Asia. Under less disturbed circumstances, these top-level predators may play an important role in controlling population densities of pigs in these forests. Both large felids are currently absent from PFR, however, and it seems unlikely that tigers and leopards will ever successfully re-colonize PFR because the reserve is too small of an area given the territory sizes of large predators. Furthermore, when dangerous animals enter the plantations surrounding the forest, they are removed by the Wildlife Department, as predicted for large carnivores inhabiting small reserves (Woodroffe & Ginsberg 1998). Support for the hypothesis that pig densities rise in the absence of predators comes from other studies in the literature; within the native range of *S. scrofa* the highest density estimates all come from areas with no extant natural predators (Table 1.1).

Even in the absence of natural predators, however, populations of prey species can only increase if enough food is present. Consequently, diet is an important consideration

in terms of population regulation and density of *S. scrofa* at PFR (Ickes & Williamson 2000; Laurance 2000). *Sus scrofa* is an omnivorous species whose diet varies greatly across habitats and geographic locations (Diong 1973; Klaa 1992). Nevertheless, in most areas the seasonal availability of large quantities of fruits and seeds is considered to be an important food source (Matschke 1964). In dipterocarp forests of Southeast Asia, mast fruiting of the majority of tree species occurs at a supra-annual scale, with little fruit fall during the intervening years (Whitmore 1984). At PFR mast fruiting occurred in 1983, 1990, and 1996. For West Kalimantan, Curran and Leighton (2000) reported that over a 520-week study period between 1986 and 1996, 95% of all dipterocarp seedfall occurred in only two six-week mast periods. Such extreme phenology severely limits the amount of fruit and seed available to pigs and may play an important role in limiting population densities under typical conditions in the region.

If food is an important limiting factor in *S. scrofa* demography in dipterocarp forests, particularly when natural predators are absent, the pig population in PFR may have reached a supranormal carrying capacity due to the proximity of African oil palm tree plantations. Oil palm trees fruit continuously, provide an extremely rich food source, and are cultivated in extensive monoculture plantations in the areas surrounding PFR. Pigs appear to make good use of this abundant food source, moving back into the reserve after feeding. Thus, in a forest where food may once have been limiting, there is currently a tremendous food supply in the surrounding area.

The supranormal pig densities at PFR result in extensive damage to understory saplings (Ickes *et al.* 2001), which may alter the future forest composition and structure within the reserve (Liu *et al.* 1999). Small reserves such as PFR are subject to severe edge effects (Gascon *et al.* 2000), particularly where edge effects operate over a large scale (Ickes & Williamson 2000; Laurance 2000).

In conclusion, *Sus scrofa* was found to occur at extremely high densities in Pasoh Forest Reserve. Though it is impossible to say for certain, it is probable that pig densities of this magnitude do not reflect historical density in this forest reserve or this forest type in general. Rather, the combination of an absence of feline predators and an abundant food supply from the surrounding agricultural plantations have allowed pigs to thrive in this area. Several studies have now documented that pigs are having strong impacts on other plant and animal species at PFR. Additional multi-species interactions in which pigs may play a role are in urgent need of investigation in this reserve.

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## CHAPTER II.

### THE IMPACTS OF NEST CONSTRUCTION BY NATIVE PIGS (*SUS SCROFA*) ON SAPLINGS IN A LOWLAND MALAYSIAN RAIN FOREST

## INTRODUCTION

Mammals may influence the demography and distribution of plant species through behaviors such as mound building or digging that result in physical disturbance (Platt 1975; Shachak *et al.* 1991; Tardiff & Stanford 1998). However, in such cases the disturbance is usually on a small spatial scale, with plant composition being altered on, in, or immediately adjacent to the disturbed area. It is much less common under natural conditions for mammal species to influence plant dynamics at a community level, particularly in forest habitats.

In fragmented forest landscapes, anthropogenic changes in and around forest fragments can drastically alter the density of mammals within the forest patches, leading indirectly to extensive changes in the plant community. For example, elephants (*Loxodonta africana*) in parts of Africa have increased in density at a local scale because logging, forest fragmentation, and fencing have forced them to concentrate foraging in smaller areas, resulting in increased tree damage and mortality, forest degradation, and retarded forest succession (Jachmann & Croes 1991, Struhsaker 1997). At Gunung Palung National Park in Borneo, extensive logging outside park boundaries changed the foraging behavior of bearded pigs (*Sus barbatus*), which specialize on the fruit and seed crops of supra-annual mast fruiting episodes (Curran & Leighton 2000). The quantity of mast produced in secondary and logged forests is drastically reduced compared to unlogged forests, which forces pigs to concentrate their feeding during masting periods in the primary forest remaining inside the park boundary, resulting in a temporary but substantial increase in local pig density. One consequence is that the dominant tree family in the 150,000-ha national park, Dipterocarpaceae, showed a complete lack of seedling recruitment over a 10-year period due to the intense seed predation by bearded pigs (Curran *et al.* 1999). Here, I document another example of negative impacts on plants caused by an elevated population density of a large mammal within a protected forest - namely, the hyper-abundance of wild pigs (*Sus scrofa*) in a rain forest reserve in Malaysia and the impacts of their nest building on the forest understory plant community.

The native range of *Sus scrofa* extends throughout Europe and continental Asia as far south and east as Peninsular Malaysia, as well as to the islands of Sumatra and Java (Oliver 1993). Throughout their range, female pigs seek shelter or construct nest sites shortly before giving birth. The amount and type of material gathered for nest building depends on environmental conditions and availability (Jensen 1989), but in most habitats young are born under dense vegetation such as shrubs or herbaceous plants gathered into a pile. In both cases the impact on the surrounding vegetation is limited. However, nest building may have a profound impact on the understory vegetation in primary lowland rain forest of Pasoh Forest Reserve (PFR) in Peninsular Malaysia for two reasons. First, there are no shrubs in the rain forest understory and herbaceous ground cover is uncommon at PFR, so female pigs predominately use woody vegetation when building nests. Females grasp 40 - 350 cm tall saplings in their jaws and twist their head to the side, either snapping the stem or uprooting the sapling entirely. Stems are then arrayed in a radial fashion over a shallow, crater-like depression in the soil, with the foliage in the center and the snapped or uprooted ends facing outward (Medway 1963). More than one individual may work to construct a nest, but on the few occasions when this was observed the second pig was much smaller, possibly a daughter of the larger pig from a previous

birth. Pigs utilized different sizes of woody plants, with larger pigs snapping off or uprooting taller, larger diameter plants. Stems that are uprooted die, but those that are snapped off may resprout from the stump that remains.

The second reason that nest building may have an unusual impact on the plant community at PFR is that wild pigs have increased dramatically in density within the reserve (Ickes In press). PFR is only 2,500 ha, too small to support populations of the natural feline predators of pigs. In addition, PFR is virtually surrounded by extensive African oil palm tree plantations which fruit continuously, providing a tremendous year-round food supply for pigs that live in the forest reserve but move into the tree plantations to feed. Pig density is 10 – 100 times historical levels and there has been a concomitant increase in the number of reproductive nests constructed annually in the forest. The combination of small reserve size, changes in land-use in the surrounding matrix, and the high mobility of pigs have created a large-scale edge effect that influences the forest understory throughout the entire reserve (Ickes & Williamson 2000).

Here, I document the incidence of nest building by *Sus scrofa* at Pasoh and quantify the impacts of this behavior on the understory plant community. The following questions are specifically addressed: (1) How many nests are constructed annually at PFR? (2) How many and what sized stems are used in nest construction? (3) How large an area is affected around each nest when pigs remove stems for construction material? (4) What proportion of tree mortality at PFR is caused directly by pigs? (5) Are certain species or taxonomic groups at greater risk than others from nest building? (6) Are nests spatially clumped, or placed preferentially in certain habitats?

## MATERIALS AND METHODS

### Site description and field methods

Fieldwork was conducted from February 1995 – October 1998 at Pasoh Forest Reserve (2° 59' N, 102° 18' E) in Peninsular Malaysia. The reserve consists of a central 650-ha of primary lowland dipterocarp forest, surrounded by 650 ha of regenerating forest selectively logged 45 – 50 years ago. The eastern extent of the reserve contains an additional 650 – 1,000 ha of primary lowland and hill dipterocarp forest. Approximately 85% of the reserve boundary is adjacent to extensive African oil palm (*Elaeis guineensis* Jacq.) tree plantations. PFR has an aseasonal climate with an average rainfall of 1,950 mm (Kochummen *et al.* 1990).

There is a 50-ha (1,000 x 500 m) plot at the center of the reserve established in 1985 – 1988 in primary forest. The plot is divided into 1,250 20 x 20 m subplots, in 50 columns of 25 subplots aligned north-south, marked with steel posts at each corner. Each subplot is marked at 5 x 5 m intervals with small yellow stakes. During plot establishment all trees  $\geq 1.0$  cm DBH (diameter at breast height) were tagged, identified, measured for DBH, and mapped. Additional surveys that recorded tree diameters, mortality, damage, and recruitment were initiated in 1990, and 1995. More than 400,000 trees have been documented in the plot, representing over 800 tree species (Kochummen 1997). In order to permanently mark trees, vinyl ribbon is used to loosely tie tags to the main stem of the sapling, either above a branch near eye-level or placed at ground level around the stem.

I conducted three surveys of pig nests in the western half of the 50-ha plot: (1) Feb – Oct 1995, (2) May – Oct 1996, and (3) May – Oct 1998. All 20 x 20 m subplots were searched in 1995, but 48 subplots (1.9 ha) were missed in 1996 and 20 subplots (0.8 ha) were missed in 1998. All pig nests located within this 25-ha area were mapped using the plot coordinate system, estimated to the nearest meter from the 5 x 5 m stakes or mapped to the nearest tree if stakes were missing. In addition, nests located outside the boundaries of the 25-ha study area were also enumerated and mapped if they contained tags from trees located within the 25-ha study area. I estimated the age of all nests based on the color of the leaves and the extent of decomposition. Three age categories were recognized and determined by the same observer in all three surveys: new, medium, and old. An attempt was made to quantify how long a nest would remain in each age category, but variables such as litterfall, rainfall or humidity, the presence of termite nests nearby, and nest size greatly affected the rate of nest decomposition or visibility and made the age classification system rather subjective. Rough estimates were that a new nest was < 2 months old, medium nests 2 – 6 months old, and old nests were created > 6 months prior to discovery. Nests were searched thoroughly for tree tags from snapped or uprooted saplings. The area around each nest was searched for tagged stumps obviously created during nest construction. All tag numbers and the locations were recorded where found, either in the nest or on a stump. For stumps with tags, I recorded mortality, resprouting, and whether or not a pig had removed the main stem or a smaller shoot.

Because tags from the 50-ha plot only provide information about trees  $\geq 1.0$  cm DBH, 10 nests were examined in detail to quantify all plants used, including those < 1.0 cm DBH. These nests were selected irrespective of size if they appeared to be < 48 hours old when discovered. The fresh condition of the stumps allowed for precise determination of which stumps had been damaged for the construction of the new nest rather than older nests in the area. At each nest all stumps were tagged, mapped, and measured for height and basal diameter (BD). Pigs usually snap saplings 20 - 60 cm above ground, so it was not possible to measure stump DBH. Instead, DBH was estimated based on stump BD (see Data analysis below).

The area around the nest from which the pig(s) took stems was delimited in the field with rope, using the stumps farthest from the nest as the outer boundary. Attempts were made to minimize the difficulty in the field of delimiting the affected area for a given nest. For example, while it would have been possible to use the convex hull of the stumps to estimate the area that pigs impact during the construction of nests, this method would have been difficult to implement in rain forest understory. Furthermore, there were various physical obstacles that pigs faced when snapping off stems up to 3.5 m tall and then dragging them to the nest site that influenced the shape of the area. It was obvious in several cases that fallen emergent trees and the large mounds of the termite *Macrotermes carbonarium* influenced which stems the pig used. A convex hull approach when roping off the affected area would have included many saplings that were essentially not available for use in construction. Consequently, subjective decisions were made in the field on a case-by-case basis when delimiting the area surrounding each nest, but attempts were made to be as consistent as possible.

Maps of stump locations were divided into 1 x 1 m subplots to estimate the total affected area from which the pig gathered stems. When the outline of the affected area passed through a subplot, if at least  $\frac{1}{2}$  the area was within the boundary that subplot was

counted as affected. Within the “affected area” all freestanding woody plants  $\geq 70$  cm tall and  $< 2.0$  cm DBH not taken by pigs were tagged, mapped, identified, and measured for BD, height, and DBH (where applicable). Diameter data for trees 1 - 2 cm DBH were available from the most recent census of the 50-ha plot. However, I also measured many of these trees in the field and used my measurements preferentially over those available from the 50-ha plot dataset when possible. In each nest all plants that had been uprooted entirely were measured and counted.

The total number of stems damaged, including those killed, within the affected area during the construction of one of the 10 nests investigated in detail includes the number of stumps plus the number of uprooted individuals found in the nest. The proportion of stems damaged for each nest within the affected area represents the total number of stems damaged divided by the total number of stems damaged and undamaged.

I investigated all plants  $\geq 70$  cm tall and  $< 2.0$  cm DBH utilized by pigs. Pigs often uproot plants smaller than this, but the impact on the overall understory structure decreases with the size of plants used. In addition, the largest pigs occasionally use woody plants  $\geq 2.0$  cm DBH but plants above this size threshold were not included in this study. To quantify the sizes of plants damaged by pigs to construct nests, plants were divided into three size classes: (1)  $\geq 70$  cm tall and  $< 0.5$  cm DBH, (2) 0.5 – 0.99 cm DBH, and (3) 1.0 – 2.0 cm DBH.

### **Data analysis**

It is important to note that analyses based on the 10 detailed nests and their affected areas included all freestanding woody plants. There are a number of woody climbers at PFR that may not begin climbing until they are 2.0 cm DBH. Consequently, some lianas were included in the dataset, even in the largest size class. Results of all analyses based on the 50-ha plot tags found in pig nests or around adjacent stumps apply only to trees  $\geq 1.0$  cm DBH because the 50-ha plot dataset does not include lianas.

In several analyses I restricted the data only to those nests from the 1996 survey. This should allow for the most precise data on trees available to pigs at the time of construction because all but two of the nests from the 1996 survey were constructed after the 50-ha plot recensus workers moved through a given area. As a result, all new recruits into the 50-ha plot, i.e. trees  $\geq 1.0$  cm DBH, had been tagged, while plot trees from previous surveys were measured with mortality or survival determined recently. In analyses for which only the 1996 pig nest survey data were used, the two nests built before that area was recensused were excluded.

### **Number of nests constructed per year**

Data from the 1996 pig nest survey were the most informative because the 1995 pig nest survey provided baseline data on nest locations for the 25-ha study area. An estimate of nests/ha/yr constructed from 1995 - 1996 (called the 1996 survey) was made using the following formula:

$$\text{(no. of total nests from 1996 * 365 days) / (no. of total days * (1/25 ha))}$$

No. of nests is the total number of nests found during the survey and no. of total days is the number of days since a given 20 x 20 m area within the 50-ha plot was searched during the previous pig nest survey totaled for all 20 x 20 m plots that were searched.

This controls for the differences in time since particular plots were searched between the 1995 and 1996 pig nest surveys, which varied from 359 – 495 days. The same formula was applied to the 1998 survey data.

### **DBH – BD regressions**

To estimate DBH from BD, generalized additive models (Hastie and Tibshirani 1990) were fit with the Splus function `gam` (Venables and Ripley 1997). The response for the DBH – BD regressions is  $p = P(y = 1)$  = (the probability that DBH/height > cutoff value), where cutoff values define the three size classes (listed above). Since the response is restricted to the interval (0,1), it was not possible to do a regular linear regression. The primary alternative is a logistic regression, where  $p = \exp(a+b*x)/(1 + \exp(a+b*x))$ , where  $x$  is BD, and  $a$  and  $b$  are the parameters of the model. However, a logistic regression is restricted to having a certain shape (namely that  $\log(p/1-p)$  is linear, and is limited in its ability to adjust to the functional form relating  $p$  to  $x$ . GAM is a more flexible nonparametric alternative.

I used a dataset of 7,000 saplings with known BD, DBH, and height from this and another study from Pasoh (Ickes *et al.* 2001). Models were fit using stems of  $BD < 5.0$  cm. The logit of the probability of being in a given size class or larger size class was related to BD, based on a smoothing spline with the number of degrees of freedom chosen by cross-validation. This method estimates the probability that an individual with a given BD is large enough to be included in each size class, using a flexible model that allows a nonlinear relationship on the logit scale. For analyses requiring classification of a stem into a single size class, rather than probabilistic proportional assignment to multiple size classes, I set cutoff values based on the smallest BD such that 50% or more of individuals were estimated to be large enough to be in the size class. Size classes were estimated from stems of  $0.10 \leq BD \leq 4.5$  cm.

Many saplings at PFR have been snapped at some time in the past by pigs but subsequently resprouted. As a result, it is not uncommon for a sapling to have a relatively large BD for its height because the new shoot has not yet attained the pre-damage height. In these cases the point of stem snap is obvious because the stem does not taper smoothly with increasing height, but rather abruptly decreases in size. Consequently, separate models for previously damaged ( $n = 1,791$ ) vs. undamaged ( $n = 5,130$ ) saplings were fit for each of the four size classes.

I expected that liana and tree saplings would have different BD-DBH relationships, but separate models for lianas and trees were not used for three reasons: (1) separate models gave quite similar fits, (2) it was not always possible to distinguish between trees and lianas, particularly for stumps that did not resprout, and (3) there were not enough lianas in each size class to fit the models.

### **Distances of stumps to nests and between nests**

Only nests located more than 20 m from the boundary of the 50-ha plot were used to calculate the distance to trees used in nest construction and the distances between nests. The coordinates of the nest were determined during the three pig nest surveys, and the coordinates for the stumps with tags and the tags found in the nests came from the 50-ha plot dataset.

I assessed whether the spatial distribution of pig nests was random by comparing the number of nests within distance  $d$  of a nest to the expected number for a Poisson process (Venables and Ripley, 1997). This was done for three datasets of nests: (1) New- and medium- aged nests from the 1996 pig nest survey (16 ha), (2) new- and medium- aged nests from the 1998 pig nest survey (20 ha), and (3) all nests from the three surveys within the plot boundaries (16 ha). That areas used in analyses are  $< 25$  ha and vary among years reflects the fact that some subplots were missed during pig nest surveys. The areas used in the analyses are the largest contiguous set of subplots that were searched for pig nests.

I also asked whether pigs chose nest locations based on local stem density. Stem density within a 10 m radius of nests from the 1996 nest survey ( $n = 136$  nests) was compared to stem density within a 10 m radius of 1,000 randomly selected points at least 10 m from the boundary of the 50-ha plot.

### **Tree species used as construction material**

I tested whether pigs used saplings of all species in proportion to their abundance in the area surrounding the nest site, using only the 1996 pig nest survey. All 1 - 2 cm trees from the tree plot based on the 1995 50-ha plot survey found within a 15 m radius of each nest from the 1996 pig nest survey were used in analyses. Whether the proportion of individuals taken was the same across species was examined using a likelihood ratio test for homogeneity of proportions within a contingency table (Fienberg 1980). The same analysis was conducted at the family level by including all individuals of species belonging to the family.

I tested whether a small number of families of interest were taken at rates significantly different than the overall proportion of individuals. The analyses consisted of a simple test for equality of proportions with binomial data. I predicted that the Ebenaceae would be taken less often because the dense wood would be difficult for pigs to bite through, and the Anacardiaceae would be taken less often because many species in this family have noxious black resin. I did not have specific predictions with regard to the Euphorbiaceae and Dipterocarpaceae, but tested them because they are the dominant plant families. Euphorbiaceae accounts for a large proportion of the tree species richness at PFR (87 species in the 50-ha plot). Dipterocarpaceae dominates the canopy and emergent strata, accounting for 25% of tree biomass (Kochummen *et al.* 1990).

### **Annual mortality of trees 1-2 cm DBH at PFR**

The differential equations of Paciorek *et al.* (2000) were used to estimate annual mortality and annual mortality plus resprouting rates of trees 1 - 2 cm DBH in the 25-ha study area. Equations were based on data from the 50-ha plot tree surveys in 1990 and 1995.

In order to estimate the number of 50-ha plot trees 1 - 2 cm taken by pigs on a per nest basis, I used the nest data from 1996 and all nests  $\geq 10$  m from the plot edge to avoid undercounting the number of individuals taken. Two nests were not used in this analysis because I suspected that they were constructed before the 50-ha plot survey crews arrived. For the remaining 134 nests, all 50-ha plot tags for trees 1 - 2 cm found in the nests and those from adjacent stumps were counted. Damaged trees were included only if they had the main stem snapped. An additional 54 tags found in nests or on stumps

that were not in the 50-ha plot dataset were included in the overall number of tags found. These tags were from sapling recruits into the 50-ha plot during the 1995 tree census. During the 1995 plot survey, all sapling recruits were tagged, mapped, and measured by survey crews, but tree diversity is so high that only a few people are capable of making identifications in the field. The separate identification crews were 4 - 24 weeks behind the survey teams, and any pig nest created during this interval could have damaged new recruits in the  $\geq 1$  cm DBH size category that were measured, mapped, and tagged but never identified. When this occurred, the saplings were subsequently removed from the 50-ha plot dataset. I therefore reinserted these data back into the 50-ha plot dataset to minimize underestimation of trees killed by pigs.

The number of 1 - 2 cm trees killed from pig nest construction in a year was estimated by calculating

$$(\# \text{ tags/nest} * \% \text{ survival}) * \# \text{ nests/yr}$$

Percent survival is the proportion of stems 1 – 2 cm DBH that were damaged by pigs during nest construction that survived to 36 months after damage occurred (Chapter 3). This number was then compared with the total number estimated to die in a year from all causes based on the 1990 and 1995 Pasoh surveys.

## RESULTS

### **Composition of individual nests**

Nest size, and consequently the area impacted, varied considerably: affected areas averaged  $244 \pm 112 \text{ m}^2$  for the ten nests, with a range of  $93 \text{ m}^2$  -  $456 \text{ m}^2$ . There was also considerable variation among the sizes of plants utilized in nest construction (Table 2.1). The percentage of plants  $\geq 70$  cm tall and  $< 0.5$  cm DBH damaged in the affected area of a nest ranged from 28 – 78%, while the extent of damage for plants 1 – 2 cm DBH was 0 - 47%. When plants from all three size classes were considered together, on average 53% of all free standing woody plants  $\geq 70$  cm tall and  $< 2.0$  cm DBH in the affected area were damaged by pigs. Of the total number of damaged plants, 45% were uprooted and killed while 55% had the main stem snapped off. Predictably, however, the percentage of plants uprooted and therefore killed outright was greater for plants of smaller stature: 54% of plants were uprooted in the smallest size category whereas only 4% of stems were uprooted in the largest class (Table 2.1).

### **Number of nests constructed per year**

Overall, 643 pig nests were enumerated within the 25-ha study area: 302 in 1995, 148 in 1996, and 193 in 1998. Eleven additional nests were recorded just outside the plot boundaries. From these 654 nests 3,480 tags from trees  $> 1.0$  cm DBH were recovered.

In the 1996 survey of the 25-ha area, 5.6 nests/ha/year were constructed, while 4.3 nests/ha/year were constructed in 1998. It is unknown how many nests were constructed and subsequently decayed prior to enumeration in each survey period. Because the 1996 survey interval was only one year, nest decay likely contributed to less underestimation of the real total than occurred for the 1998 survey. Even so, a number of new and medium aged nests from 1995 had disappeared within a year, suggesting that the observed 5.6 nests/ha/year is indeed an underestimate. For the 1996 – 1998 survey interval, nest decay occurring during the 24-month interval means that that the observed

Table 2.1 Average number of woody stems that were snapped, uprooted, and undamaged within the affected areas of 10 pig nests at Pasoh Forest Reserve, Peninsular Malaysia.

Size class	No. snapped	No. uprooted	No. total damaged	No. undamaged saplings	% of total stems damaged
70 cm tall < saplings < 0.5 cm DBH	88.0 ± 45.4	113.4 ± 58.5	201.4 ± 80.6	142 ± 72.9	58.9 ± 15.0
saplings 0.5 – 1.0 cm DBH	32.9 ± 13.8	7.3 ± 4.3	40.2 ± 16.5	36.2 ± 23.0	53.6 ± 13.3
1.0 – 2.0 cm DBH	24.4 ± 16.7	0.9 ± 1.1	25.3 ± 17.4	67.6 ± 30.9	25.4 ± 14.9
all plants	145.3 ± 49.1	121.6 ± 59.9	266.9 ± 85.7	245.8 ± 115.1	53.0 ± 9.9

4.3 nests/ha/year is a conservative estimate for the period from 1996 to 1998. Therefore, to account for decayed nests as well as those missed in the survey, I use 6.0 nests/ha/year as the best estimate of the number of nests constructed between 1995 and 1996 in the equations for estimating mortality of trees due to pigs (see below).

### **Distances of stumps to nests and between nests**

Pigs gathered woody stems from relatively close to the nest site. More than 80% of trees > 1 cm were obtained within 10 m of the nest and 95% obtained within 15 m away (Fig. 2.1).

It is apparent that pigs avoided constructing nests adjacent to the three major trails within the 25-ha study area, particularly where the two largest trails intersect (Fig. 2.2). Also, the extreme Northeast portion of the study area represents the only non-flat area surveyed, and pigs may have built less frequently on the slopes. Aside from avoiding areas near the trails and possibly slopes, nests were observed throughout the study area.

Nests from 1996 were clumped at distances of 30 - 170 m (Fig. 2.3), while nests from 1998 were clumped at distances > 40 m (Fig. 2.4). For all the nests combined, there was significant clumping at distances > 30 m but the degree of clumping appears to be less than when focusing on specific years. This suggests that nest-building activity in a given year is concentrated in certain areas within the plot, although it appears to be random at small scales. It is not known if the clumping seen for all the nests combined is primarily because of the path avoidance by the pigs. Most nests were within 30 m of the nearest nest within a survey period, but rarely within 10 m (Fig. 2.5).

Pigs did not choose nest site locations with stem densities different from the plot. Based on 1000 locations, the mean density of stems 1- 2 cm was 77.0 per 10 m radius circle (S.D. = 27.7). The mean for the 1996 nest locations was  $74.9 \pm 4.7$  (2 SE).

### **Annual mortality of trees 1-2 cm DBH at PFR**

Overall annual mortality of trees 1 - 2 cm from all causes was estimated to be 1.84%, and trees suffering stem snap damage or being killed was 3.52% annually.

The 816 tags from the 134 pig nests in 1996 gave an estimate of 6.1 trees 1 - 2 cm per nest. Using our estimate of 6.0 nests/ha/year, 36.5 individuals were killed or damaged per year because of pig nest construction. I assumed that 35.6% of damaged individuals die (Chapter III), which gave an estimate of 2.1 deaths/nest/year, or 13.0 deaths/ha/year.

Based on the annual mortality rates computed above for trees 1 - 2 cm and 2,471.4 stems 1 - 2 cm/hectare, there were an estimated 45.5 deaths and 85.5 deaths plus resprouts per hectare in this size class. This suggests that trees killed for pig nest construction comprised 29% (13.0/45.1) of the total mortality due to all causes and 43% (36.5/85.5) of total mortality and resprouting combined. Annual mortality for pigs alone was 0.53% for trees 1 - 2 cm at Pasoh Forest Reserve.

### **Tree species used as construction material**

For the 1996 survey, 833 or 3.4% of trees 1 - 2 cm were taken of 24,396 available. There was no evidence for species-level differences in the proportion taken ( $G^2 = 611$ ,  $df = 622$ ,  $P = 0.62$ ), but it is important to note that sample sizes were small for

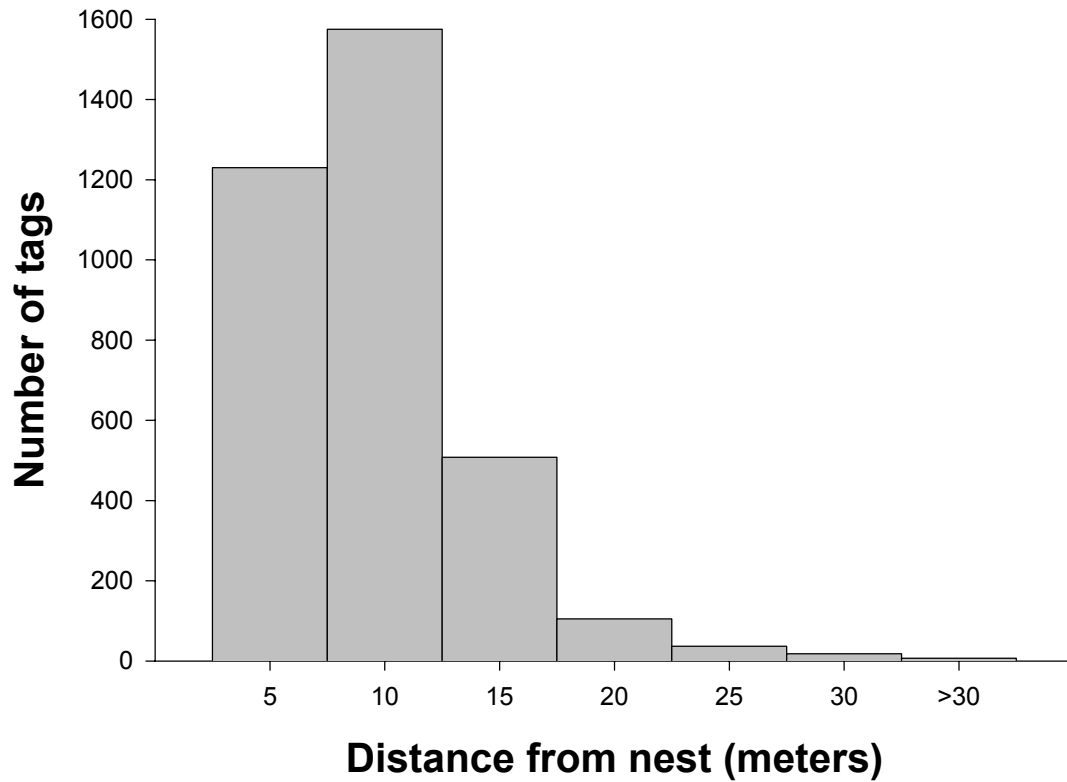


Figure 2.1 The distance from pig nests to the locations of the 3,480 trees  $\geq 1.0$  cm DBH used in construction. Tree coordinates come from the 50-ha dataset and nest coordinates were mapped during surveys in 1995, 1996, and 1998. Distances for trees with tags found in nests were calculated as a straight line from the nest to the position of the tree. When two or more nests of similar age were close together, stumps were assumed to have been used in the construction of the nearest pig nest.

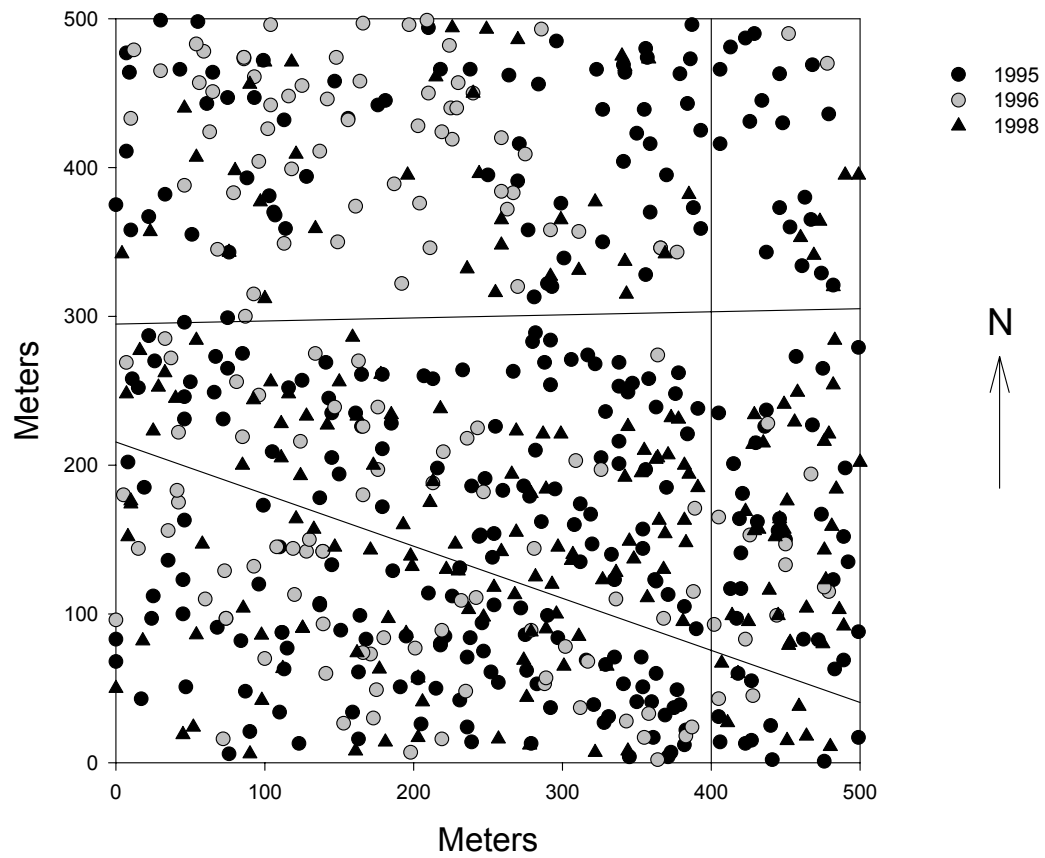


Figure 2.2 Locations of all pig nests found within the 25-ha study area during all three surveys at Pasoh Forest Reserve, Peninsular Malaysia. Solid lines indicate trails in the area.

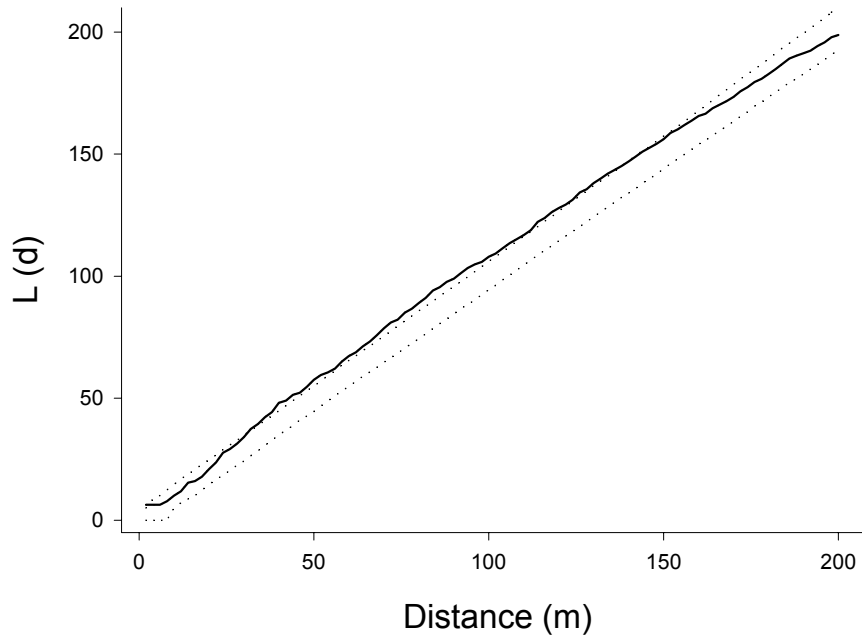


Figure 2.3 Analysis of clumping of pig nests from the 1996 survey. The figure shows confidence intervals that are simulated based on assuming a Poisson process but fixing the number of points at the actual number of nests observed.  $L(d) = \sqrt{K(d)/\pi}$  where  $K(d)$  is Ripley's K function. For a Poisson process,  $L(d)$  is linear in  $d$ , such that values of  $d$  for which  $L(d)$  is above the confidence bands indicate significant clumping at  $P > 0.05$  at that distance scale.

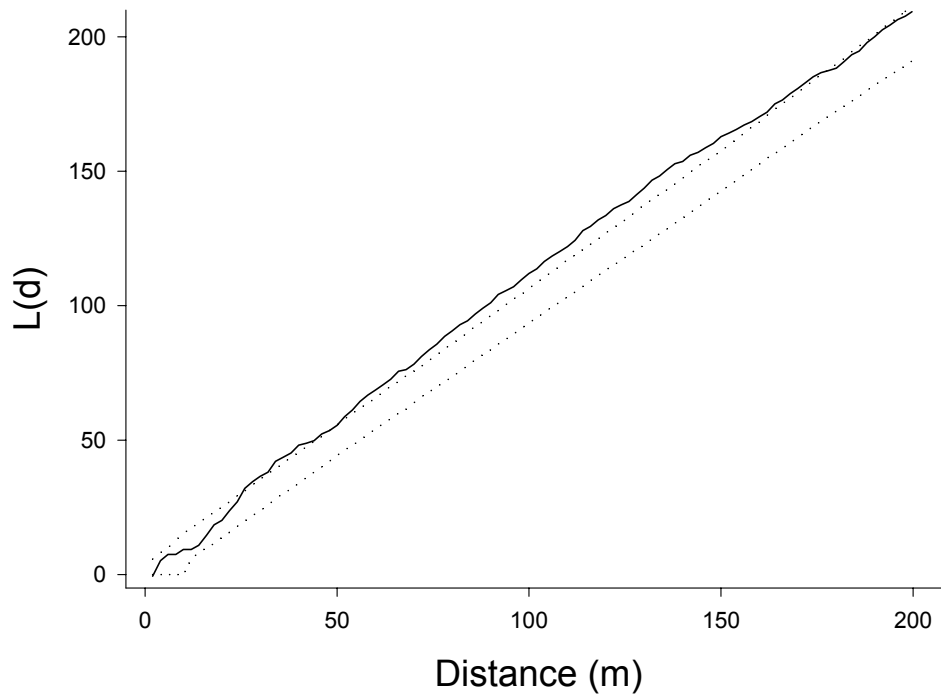


Figure 2.4 Analysis of clumping of pig nests from the 1998 survey. The figure shows confidence intervals that are simulated based on assuming a Poisson process but fixing the number of points at the actual number of nests observed.  $L(d) = \sqrt{K(d)/\pi}$  where  $K(d)$  is Ripley's K function. For a Poisson process,  $L(d)$  is linear in  $d$ , such that values of  $d$  for which  $L(d)$  is above the confidence bands indicate significant clumping at  $P > 0.05$  at that distance scale.

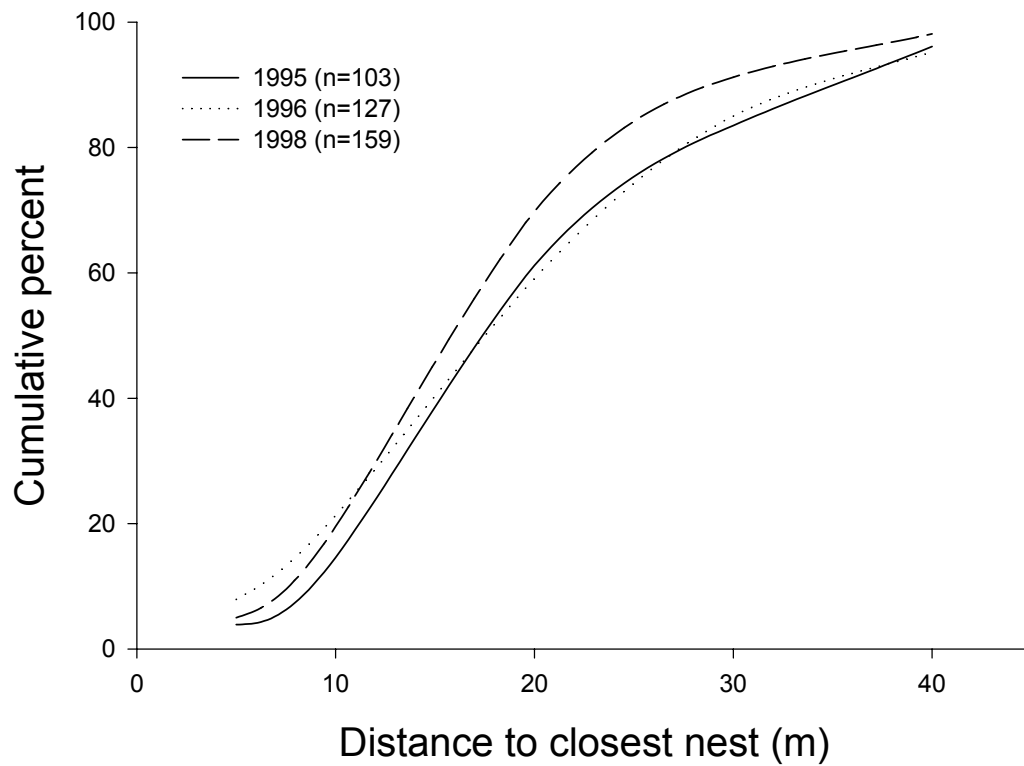


Figure 2.5 The proportion of pig nests within x meters of the nearest nest within the same survey period. Sample sizes of nests are given parenthetically. Only pig nests of “new” and “medium” ages were considered for 1995, but all nests were used for 1996 and 1998.

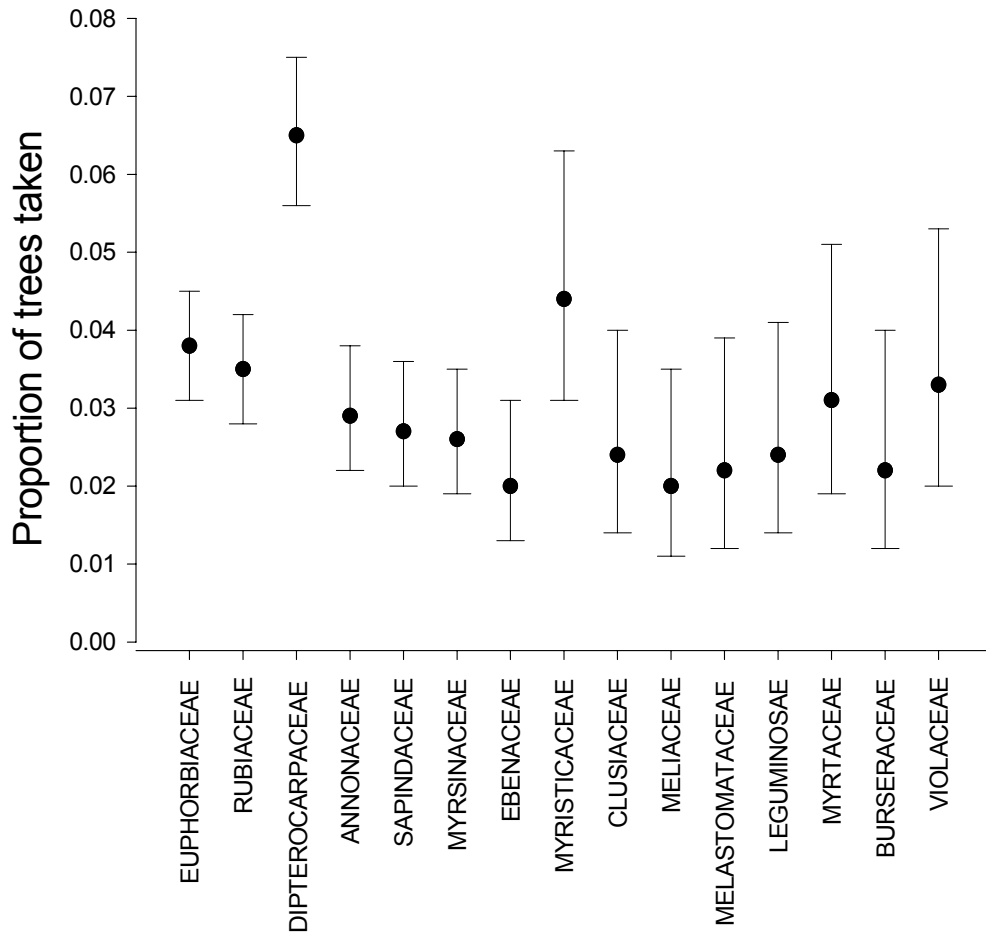


Figure 2.6 Proportion of stems within a 15-m radius of each pig nest that were in used nest construction. All nests from the 1996 survey were used in calculating the proportion taken. Families are arranged from left to right on the x-axis in decreasing order of the number of stems from that family available to pigs for nest construction: 2,970 saplings 1 - 2 cm DBH were available from the Euphorbiaceae while 515 were available from the Violaceae. Only families with > 500 stems available are shown. Bars represent the 95% confidence interval of the proportion taken. Confidence intervals are based on the normal approximation to the binomial distribution with continuity correction.

each species due to the extraordinary diversity in this forest. There were large differences in the proportion of individuals taken at the family level ( $G^2 = 135$ ,  $df = 69$ ,  $P < 0.0001$ ; Fig. 2.6). Individuals from the Dipterocarpaceae were used in nest construction more frequently (6.5%) than all trees combined (3.4%;  $P < 0.0001$ ). The most common dipterocarp species at PFR, *Shorea maxwelliana*, accounted for 40% of all dipterocarps damaged and had 6.6% of stems damaged within affected areas. However, 6.4% of the stems from the other dipterocarp species available were also taken, suggesting that all dipterocarps were chosen preferentially over non-dipterocarp species. As predicted, trees in the Ebenaceae, all in the genus *Diospyros*, were taken less frequently than all trees combined (2.0% vs. 3.4%;  $P = 0.01$ ), but there were no differences in the proportion taken for the Euphorbiaceae (3.8% vs. 3.4%;  $P = 0.29$ ) or Anacardiaceae (3.8% vs. 3.4%;  $P = 0.73$ ).

## DISCUSSION

The building of reproductive nests by pigs is potentially having a profound impact on the understory vegetation at Pasoh Forest Reserve. During the three surveys, over 600 pig nests were encountered in the 25-ha study area, with an estimated 6.0 nests/ha constructed annually. Nests were constructed throughout the study area overall, though they were somewhat spatially clumped within surveys. On average, each nest constructed affected an understory area of 244 m<sup>2</sup> and was composed of 262 saplings  $\geq 70$  cm tall and  $< 2.0$  cm DBH: 117 saplings were uprooted and 145 had stems snapped. Within the 244-m<sup>2</sup> affected areas, 53% of all freestanding woody plants in this size range were damaged or killed by pigs.

When only trees 1 - 2 cm were considered, all species appeared to be susceptible to pigs as nest construction material. Species suffered in proportion to their abundance within the area affected, though at the familial level Dipterocarpaceae, the most dominant family at PFR, was taken twice as often as expected by chance and more often than any other family. Nests accounted for 28.9% of the overall mortality and 42.7% of the mortality plus damage in the study area for trees in the 1 - 2 cm size class.

### **Tree mortality at PFR due to pigs**

Pigs alone caused 0.53% annual mortality of trees 1 – 2 cm at PFR. This is a remarkably high mortality rate attributed to a single causal agent as annual mortality generally ranges from 1 – 3% in tropical forests (Phillips *et al.* 1994). The only other examples of mammals known to cause comparable tree mortality and damage are beavers through foraging and dam building and subsequent changes in hydrology in the temperate zone, and locally dense populations of elephants through foraging and trampling in the tropics (Barnes & Dibble 1988; Naiman *et al.* 1988; Struhsaker *et al.* 1996; Struhsaker 1997; Donkor & Fryxell 1999).

Although the data suggest that pigs are playing a large role in understory plant dynamics, the results, nonetheless, underestimated the damage caused by pigs for two reasons. First, it is unlikely that I encountered all pig nests during the 25-ha surveys. Second, a considerable number of tags from trees damaged or killed by pigs may not have been found. Despite thorough searches, it was easy to overlook tags in the nests among the large quantity of decomposing vegetation or at the base of stumps.

Furthermore, when a pig drags a tree towards the nest the tag may slide off the base of the stem. I chose to ignore tags on the ground more than a meter from a pig nest because when a tree dies from any cause in the 50-ha plot tags are intentionally left on the forest floor for subsequent censuses.

It is also important to note that only damage to freestanding woody plants was documented in this study. Pigs clearly prefer to use leaves of understory, broad-leaved monocot species when available, particularly from the palm genus *Licuala* and terrestrial gingers and aroids. Unfortunately, there are no demographic background data on these groups of plants at PFR. Though broad-leaved understory plants are currently rare at PFR, this rarity is possibly due to pigs using them preferentially as nesting material. I am aware of no other lowland Dipterocarp forest in Peninsular Malaysia with such a low density of understory, broad-leaved monocots.

The number of pig nests constructed annually is presumably a function of pig density. Ickes (In press), using line transect surveys, estimated pig density at PFR in 1996 and 1998 as 47 and 27 pigs/km<sup>2</sup>, respectively. The difference between years was attributed to a greater number of young pigs in 1996, the number of observed adults being almost identical between years. Year 1996 was a mast-fruiting year, with fruit fall mostly in September – October, and there were almost four times as many new reproductive nests that year compared with 1998. Nonetheless, when all nests found during the surveys were included the nest density was 5.6 in 1996 vs. 4.3/ha/year in 1998, a difference of only 23%. Given that there was a survey of nests in 1995 but not 1997, there were approximately 12 months for nests to have been built and subsequently enumerated in 1996 but 24 months prior to the 1998 survey. During this 24-month interval a number of nests were likely built that then decayed before they were enumerated. I am unable to estimate how many nests may have decayed during this interval, but it was probably enough to raise the estimate of number of nests/ha/year for the 1996 – 1998 interval to a level comparable with the 5.6 nests/ha/year during the 1995 – 1996 interval.

There have been no studies on the biology of *Sus scrofa* in Southeast Asian rain forests. Consequently, it is unknown how closely tied their reproductive biology is to mast fruiting events, whether they nest seasonally or year-round, or if they have one or two litters per year. At PFR I have observed new nests constructed in all months, but this may be a function of the continuous oil palm fruit supply for pigs at Pasoh and does not indicate that natural breeding occurs year-round.

The congeneric bearded pig (*Sus barbatus*), which also constructs reproductive nests, occurred sympatrically with *Sus scrofa* in much of Peninsular Malaysia and Sumatra until the last few decades (Medway 1983). Bearded pigs are thought to be nomadic, migrating across large distances and tracking mast-fruiting events on a regional scale (Caldecott *et al.* 1993). They have declined dramatically in Peninsular Malaysia due to extensive deforestation and much of their current range and movements remain undocumented. Only one group, comprising 18 individuals and seen only once, was observed at Pasoh during this study (pers. obs). As mentioned previously the current density of *Sus scrofa* at PFR is extremely high compared with historic levels. However, until very recently there would have been two Suid species constructing reproductive nests in lowland dipterocarp forests in Peninsular Malaysia. While probably not as dramatic as currently at PFR, nest building by pigs may nonetheless have been an

historically important component of understory plant dynamics in this and other lowland rain forests in Peninsular Malaysia and Sumatra.

### **Pig nests as understory gaps**

The average understory area affected by pig nests at PFR was 244 m<sup>2</sup>. Within this area, pigs removed or severely damaged > 50% of the understory woody vegetation, essentially creating an understory gap (*sensu* Connell *et al.* 1997). The area affected per nest was the equivalent of a “large” canopy gap, and was larger than 76% of canopy gaps from Barro Colorado Island in Panama and 95% of canopy gaps at La Selva, Costa Rica (Brokaw 1982; Sanford *et al.* 1986). Whereas canopy gaps result in dramatic increases in light and temperature, alter soil nutrient and water conditions, and decrease competition for light and nutrients (Denslow 1987), such changes are comparatively small in the understory gaps of pig nests because only understory plants are damaged. Although Connell *et al.* (1997) reported that growth rates are often higher even in understory gaps, this may not be the case for understory gaps at PFR. I followed pig-created stumps for 36 months after nest construction and found remarkably slow growth rates (Chapter 3). In areas of high nest abundance at PFR virtually all remaining understory plants are either too big to be used by pigs in nest construction (> 2.5 cm) or are short stumps with slowly growing resprouts. Furthermore, in a separate study, Ickes *et al.* (2001) constructed pig exclosures at PFR and found that growth rates were higher inside fences to which pigs had no access, a result attributed to negative effects of soil disturbance in control plots by pig rooting. This suggests that the detrimental effects on plant growth by soil disturbance via pig rooting may ameliorate some of the expected advantages to saplings undamaged during nest construction.

Estimates for conversion of forest to canopy gaps range from 0.7 – 1.2% per year (Denslow 1987). The 6.0 pig nests/ha/year created at PFR affected 1,366 m<sup>2</sup>, or 1.4% of the area. As a result, pig nest building is impacting annually an understory area at least as large as that affected by canopy gap formation. In this study I documented the impacts of nest building on the plants damaged in the construction process, but how the considerable decrease in understory biomass affects other organisms and processes remains to be investigated.

### **Pigs and edge effects**

The current extreme density of *Sus scrofa* at PFR is a function of both area and edge effects. In terms of reserve area, at only 2,500-ha PFR is too small to support populations of large carnivores such as tigers and leopards. Although the number of pigs could certainly feed large carnivores if they re-colonized PFR, when large cats wander outside the forest they are removed by the Wildlife Department as dangerous to the workers in the oil palm plantations around and adjacent to the reserve. In terms of an edge effect, the extensive oil palm agricultural plantations provide a constant, high-calorie food supply for pigs that live in the forest but move outside for feeding. In this scenario, the extent of the edge effect is determined by the mobility of pigs: even the center of PFR is < 2 km from an agricultural area, easily within the mobile range of pigs. As a result, pigs throughout the reserve may be accessing this food source, such that pig density, and consequently pig nest building, is high throughout the reserve (Ickes & Williamson 2000).

Pasoh is almost certainly not a unique situation in Malaysia. More than 25% of the entire area of Peninsula Malaysia is in tree plantations of either rubber (*Hevea brasiliensis*) or African oil palm, and most rubber plantations have been or are currently being converted to oil palm due to the collapse of the rubber market. As a result, many forest reserves or unprotected forest fragments are adjacent to oil palm plantations. While I am aware of no other studies of *Sus scrofa* in Malaysia, given the small size of most reserves and their proximity to oil palm plantations, it seems likely that pig density, and hence nest building activity, may be elevated throughout Peninsular Malaysia.

### **Changes in forest composition at PFR**

*Sus scrofa* was found to use saplings from the Dipterocarpaceae preferentially when constructing nests, and one possible mechanism for this preference is olfactory association with the family that also provides a major source of food. Pigs consume mast throughout their range, and in Southeast Asia the most important masting family is the Dipterocarpaceae. Most dipterocarps produce large quantities of fruit (mast) on a supra-annual scale of 3 - 7 years. Pigs have a well-developed sense of smell used constantly while foraging, and they may associate dipterocarp saplings, if not with food, at least with a relatively safe group of plants.

Regardless of the mechanism, dipterocarp species were damaged more frequently than species from other families. In addition, in another study I followed > 1,450 stumps created by pigs during nest construction and 350 created experimentally to determine if plant taxa show different abilities to resprout following stem snap damage (Chapter III). Survivorship of resprouting stumps was compared with survivorship of adjacent undamaged saplings from the same family; after 36 months, dipterocarps had the lowest survivorship of the 19 plant families tested. Dipterocarps comprised 24% of aboveground plant biomass at PFR in 1990. However, if pig density and the number of nests constructed annually at PFR remains elevated their may be an ongoing shift away from dominance by the Dipterocarpaceae in favor of species that are either less often used in nest construction or that can resprout successfully from the stumps left behind.

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### CHAPTER III.

#### RESRPOUTING OF WOODY SAPLINGS FOLLOWING STEM SNAP BY WILD PIGS IN A MALAYSIAN RAIN FOREST

## INTRODUCTION

Woody plants are subjected to various types of physical disturbance that lead to loss of foliage or stems. The relative ability of a species to resprout subsequent to disturbance events should be directly correlated to the frequency and intensity of the disturbance. In tropical forests 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, understory woody plants still experience significant stem damage from small-scale disturbances such as branchfalls and treefalls (Aide 1987; Clark & Clark 1991). Consequently, the ability to resprout should be a common plant characteristic even in areas that rarely experience large-scale disturbances. 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 understory plants in lowland dipterocarp rain forest at Pasoh Forest Reserve (PFR) in Peninsular Malaysia, where nest building by native wild pigs (*Sus scrofa*) is an additional source of physical damage to saplings.

Pigs everywhere build nests to some degree, but the importance of this behaviour on understory plant dynamics at PFR is higher than elsewhere within the range of *Sus scrofa* for two reasons. First, in other regions or habitats herbaceous plant material is used in nest construction with less impact on surrounding vegetation. However, there are few herbaceous plants in the understory 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 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 In press). The increase is attributed to the absence of large predators and an abundant year-round food supply in the agricultural areas that surround the 2,500-ha forest reserve. A consequence of high pig density is that the number of nests constructed by pigs is also quite high. From 1996 - 1998 there were 560 pig nests constructed/km<sup>2</sup>/year, damaging an estimated 173,000 saplings/km<sup>2</sup>/year. Of these saplings, 51% were uprooted and died, whereas 49% had stems snapped and may therefore resprout (unpubl. data).

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 a selective 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 all tree species within a selected size range in proximity to their nests. *Sus scrofa* at Pasoh shows no species-specific preferences in saplings utilized during nest building: all woody species suffer in proportion to their abundance within the area affected (unpubl. data). Species may differ in their ability to resprout following physical disturbance as a consequence of differing patterns of meristematic capacity, root-shoot partitioning, stored carbohydrate and nutrient reserves, and other factors (Zimmerman *et al.* 1994). Thus, the overall impact of pig-related disturbance on forest composition is likely to result mainly from differences in the ability of tree species to resprout following stem snap.

To investigate resprouting of understory plants, we followed all stumps created by pigs in the construction of 10 nests and stumps created experimentally for 36 months. We determined the overall proportion of saplings that resprouted following stem snap in this forest, and whether resprouting ability was associated with physical characteristics of saplings such as height, diameter, and the presence of leaves remaining after damage. We also evaluated the relative importance of a variety of morphological and life-history characteristics as correlates of resprouting, including relative species abundance, growth habit (trees vs. lianas), leaf morphology, tree size at maturity, and tree taxonomic affinity.

## MATERIALS AND METHODS

### Study system

Pasoh Forest Reserve is located 110 km Southeast of Kuala Lumpur, Malay Peninsula (2° 59' N, 102° 18' 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 - 1959, and another 650 - 1,000 ha of primary hill dipterocarp forest. Aside from a corridor of hill forest that connects PFR to the southern end of the main mountain range of Peninsular Malaysia, the remaining perimeter (approximately 85%) abuts mature African oil palm (*Elaeis guineensis* Jacq.) tree plantations established in the 1970's. The flora of PFR is exceptionally diverse, with over 800 tree species  $\geq 1.0$  cm DBH (diameter at breast height) recorded in a 50-ha plot (Kochummen 1997). Annual rainfall is approximately 2,000 mm with a known range of 1,700 - 3,200 mm (Kochummen *et al.* 1990). Monthly rainfall means exceed 100 mm, providing an aseasonal climate.

### Stumps created during nest construction

Ten new pig nests were located in the understory 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. Each nest was thought to be less than 48 hours old at the time of discovery (10 June - 5 Nov. 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, shoot height above ground, 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, not including any branches below the point of stem snap that were present before damage occurred. Thus TSL includes only new growth. With few exceptions, it was not possible to identify stumps that did not develop resprout shoots. Plants were recorded as dead if there were no leaves or shoots present and the wood was dry and brittle to the touch. Also, even if a stump appeared healthy but had no visible vegetative growth during one census and was dead during the next survey period, it was recorded as dead during the first survey.

To compare mortality of stem snapped versus 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.

### **Stumps created experimentally**

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 x 5 m transects approximately 500 meters apart, divided them into eight 5 x 5 m plots, and measured and identified all trees  $\geq 60$  cm tall. In alternate plots plants  $\geq 60$  cm tall and  $\leq 2.5$  cm DBH were cut with a machete 20 - 60 cm above the ground. These plants were in the size range 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 revisited at 3, 6, 12, and 36 months with the same measurements taken as those for stumps created by pigs. Transects were located 20 meters inside and were parallel to 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 the arboreal cover of oil palm trees in the surrounding plantations (S. Thomas unpublished data).

In addition to stump physical characteristics measured in the field (BD, stump height, and presence/absence of leaves remaining on the stump), 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 DBH, 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. “Treelets” were defined as species that seldom attain 2.0 cm DBH. “Understory” species were those that regularly reach maximum DBH 2 - 10 cm, “midstorey” 10 - 30 cm, and “canopy”  $> 30$  cm. A classification based on height would have been most appropriate, but little information exists on species-specific maximum heights for tropical trees. Lianas were excluded from all analyses where stratum was an independent variable.

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  $> 2,000$  stems were considered “abundant” ( $n = 29$ ), species with 1,000 – 2,000 stems were “common” ( $n = 42$ ), 500 – 1,000 stems were “uncommon” ( $n = 46$ ), and  $< 500$  stems were “rare” ( $n = 73$ ). It was not possible to obtain reliable information regarding the abundance’s of treelet species below the 1.0-cm DBH threshold of the 50-ha plot. Therefore, to categorise treelets data from other studies conducted concurrently at PFR provided information on 1959 individuals  $\geq 70$  cm tall and  $< 1.0$  cm DBH (e.g. Ickes *et al.*, 2001). Based on this sample, treelet species that had  $> 30$  stems 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 also excluded from all analyses using abundance as the independent variable.

## Data analysis

SAS version 8.0 (SAS Institute 1997) was used for statistical analyses. Significance levels were set at  $\alpha = 0.01$  because a large number of tests were conducted. 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 effect on survivorship of all variables was examined with likelihood ratio chi-square tests of independence (PROC GENMOD, using a binomial distribution and logit link function). 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 analyzed separately. Tests were performed with all species combined and separately for the 13 species that had at least 16 identified stems. The survivorship of each of these 13 species was tested against survivorship of conspecific, undamaged individuals around the pig nests and in the alternate 5 x 5 m plots of the experimental stump transects. Similarly, family-level differences in survivorship were tested between damaged individuals and undamaged plants in the same family.

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 not test if compound- and simple-leaved individuals survived pig damage to the same degree at 3 months. This test was performed 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. The same holds true for all comparisons. 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 were examined by focusing on TSL. The effect of each class variable on TSL was examined using non-parametric analysis of variance (Kruskal-Wallis chi-square) because of consistent violations of the Shapiro-Wilk test for normality when parametric tests were used. Continuous variables (BD and stump height) were correlated with TSL using Spearman rank correlations. Number of resprout shoots per species was examined using a Poisson distribution (PROC GENMOD, Poisson distribution with a log link). Individuals with no new shoot growth were excluded for analyses of TSL.

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, abundance).

## RESULTS

There were a total of 1,808 stumps examined for resprouting: 1,477 created by pigs and 331 created experimentally. Of the total, 78% ( $n = 1,405$ ) of the individuals were identified to 257 species or morphospecies and 80% ( $n = 1,445$ ) were identified 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 ~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% of these had not produced any new shoots and 41.5% had not produced any 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**

Pig and experimental stumps did not differ in production of at least 2 cm of shoot growth by 3 months ( $\chi^2 = 0.6$ ,  $df = 1$ ,  $P = 0.42$ ), in production of a fully-expanded leaf at 3 months ( $\chi^2 = 3.4$ ,  $df = 1$ ,  $P = 0.07$ ), or in the probability of surviving to 3 months ( $\chi^2 = 0.2$ ,  $df = 1$ ,  $P = 0.69$ ), 6 months ( $\chi^2 = 0.0$ ,  $df = 1$ ,  $P = 0.89$ ), or 12 months ( $\chi^2 = 4.0$ ,  $df = 1$ ,  $P = 0.05$ ). Percent survival to 36 months, however, was higher for experimental (73.1%) than pig stumps (65.2%) ( $\chi^2 = 8.1$ ,  $df = 1$ ,  $P = 0.005$ ). Experimental stumps also had 22 – 40% greater TSL at each time interval. Both BD ( $\chi^2 = 26.5$ ,  $df = 1$ ,  $P < 0.0001$ ) and height ( $\chi^2 = 227.6$ ,  $df = 1$ ,  $P < 0.0001$ ) were significantly higher for experimental stumps, indicating that the experimental stumps were representative of the larger stems affected by pigs. Because size-dependent patterns in resprouting were similar between pig and experimental stumps, 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. 3.1). At 36 months 67% of all stumps were alive, whereas 91% of undamaged saplings survived to this time period ( $\chi^2 = 387.3$ ,  $df = 1$ ,  $P < 0.0001$ ). When the experimental stumps were excluded, the survivorship 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.

Initial stump physical characteristics strongly affected survivorship, particularly at early time intervals. Basal diameter was positively related to survivorship at 3, 6, and 12 months but had no significant relationship to survivorship at 36 months (Fig. 3.2a). Stump height was positively related to survivorship at all time intervals (Fig. 3.2b). However, stump height was positively correlated with stump BD ( $R^2 = 0.46$ ), and when both were considered in a single model, BD was strongly correlated with survivorship at 3 and 6 months but not at 12 and 36 months, whereas stump height was not correlated with survivorship at any time interval (data not shown). The presence of leaves below the point of damage did not affect survivorship at any time interval (data not shown), though stumps with leaves were rare (only 68 stumps had leaves remaining on the stump whereas 1,740 did not). Thus, BD seems to be the more important initial stump characteristic determining initial survival probabilities after stem damage.

Several natural history parameters were also significant predictors of sapling survivorship following damage. Stratum of adult trees was significantly related to individual stem survivorship at 6, 12, and 36 months (Fig. 3.3a). At all three time intervals species from lower strata were more likely to be alive and canopy species had considerably lower survivorship than treelets, understory, or midstorey species. Abundance was significantly related to survivorship only at 6 months, at which time rare and uncommon species had greater mortality than common or abundant species

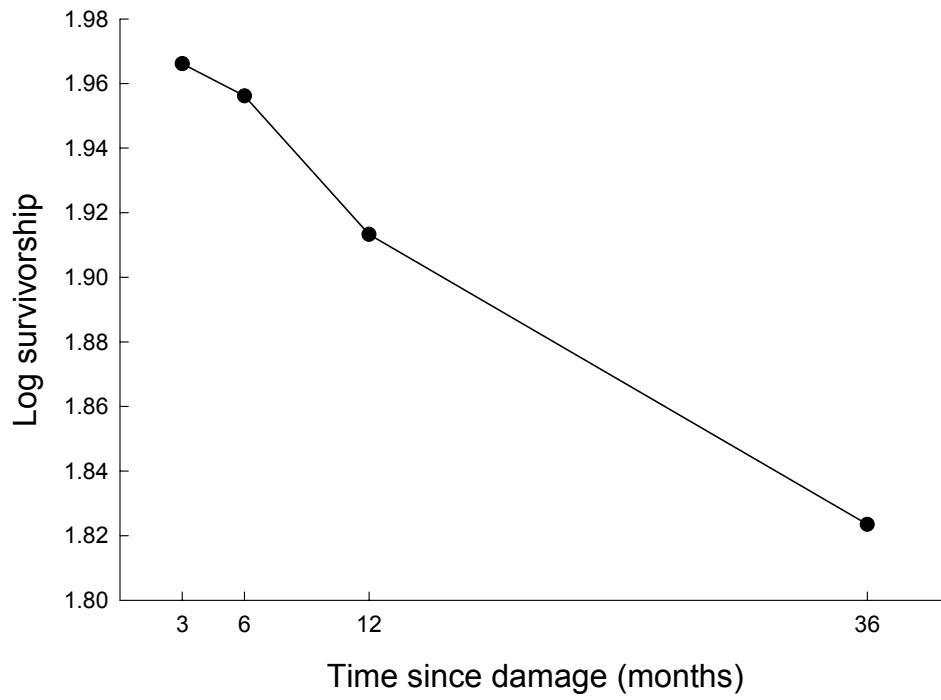


Figure 3.1 Log survivorship of pig-damaged saplings over time at Pasoh Forest Reserve, Malaysia.

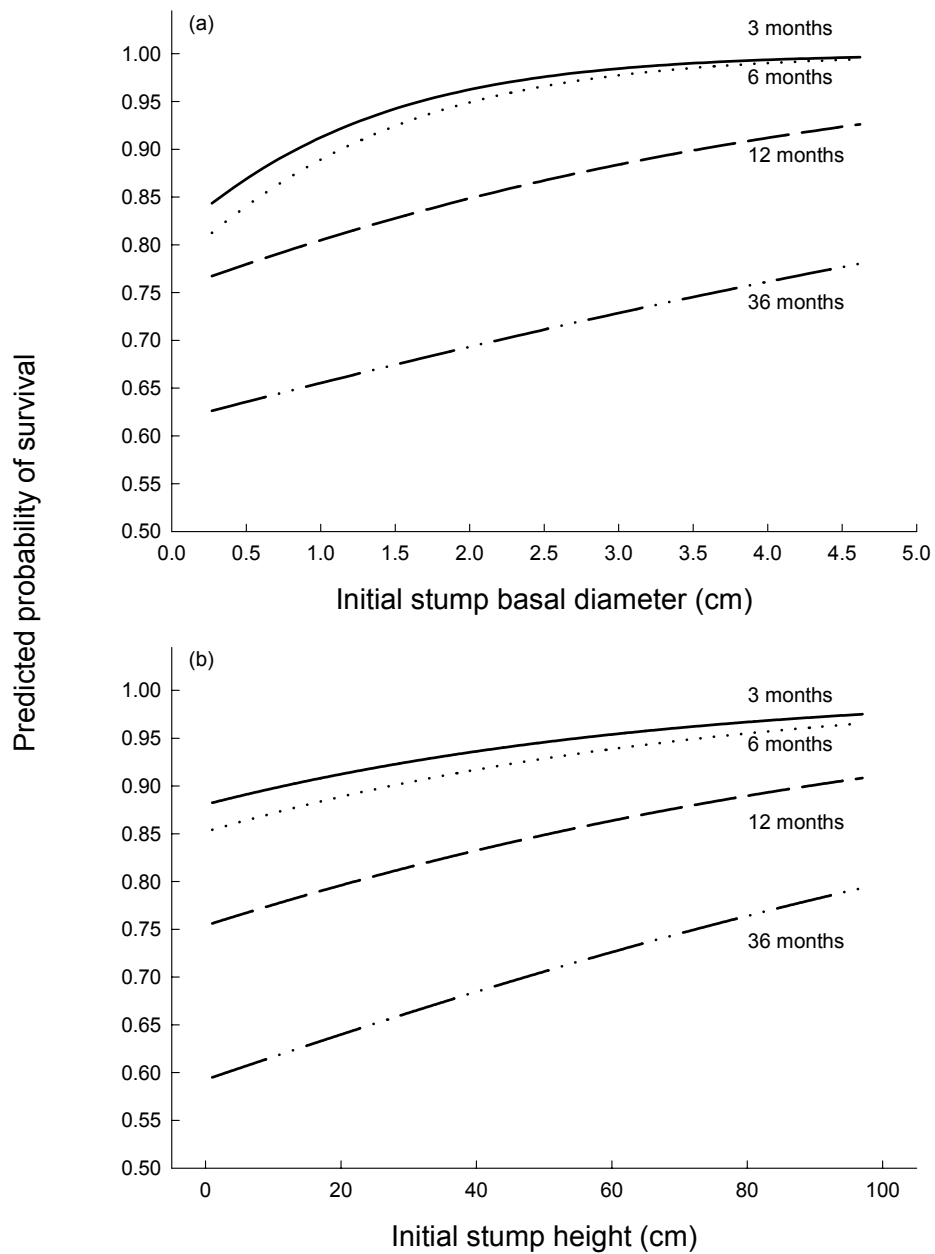


Figure 3.2 Predicted probability of stump survival at 3, 6, 12, and 36 months post-damage at Pasoh Forest Reserve, Malaysia in relation to (a) BD at 3 ( $\chi^2 = 19.3$ ,  $df = 1$ ,  $P < 0.0001$ ), 6 ( $\chi^2 = 21.7$ ,  $df = 1$ ,  $P < 0.0001$ ), 12 ( $\chi^2 = 6.0$ ,  $df = 1$ ,  $P = 0.01$ ), and 36 months ( $\chi^2 = 3.1$ ,  $df = 1$ ,  $P = 0.08$ ) and (b) stump height at 3 ( $\chi^2 = 6.6$ ,  $df = 1$ ,  $P = 0.01$ ), 6 ( $\chi^2 = 7.5$ ,  $df = 1$ ,  $P = 0.006$ ), 12 ( $\chi^2 = 7.5$ ,  $df = 1$ ,  $P = 0.006$ ) and 36 months ( $\chi^2 = 7.8$ ,  $df = 1$ ,  $P = 0.005$ ).

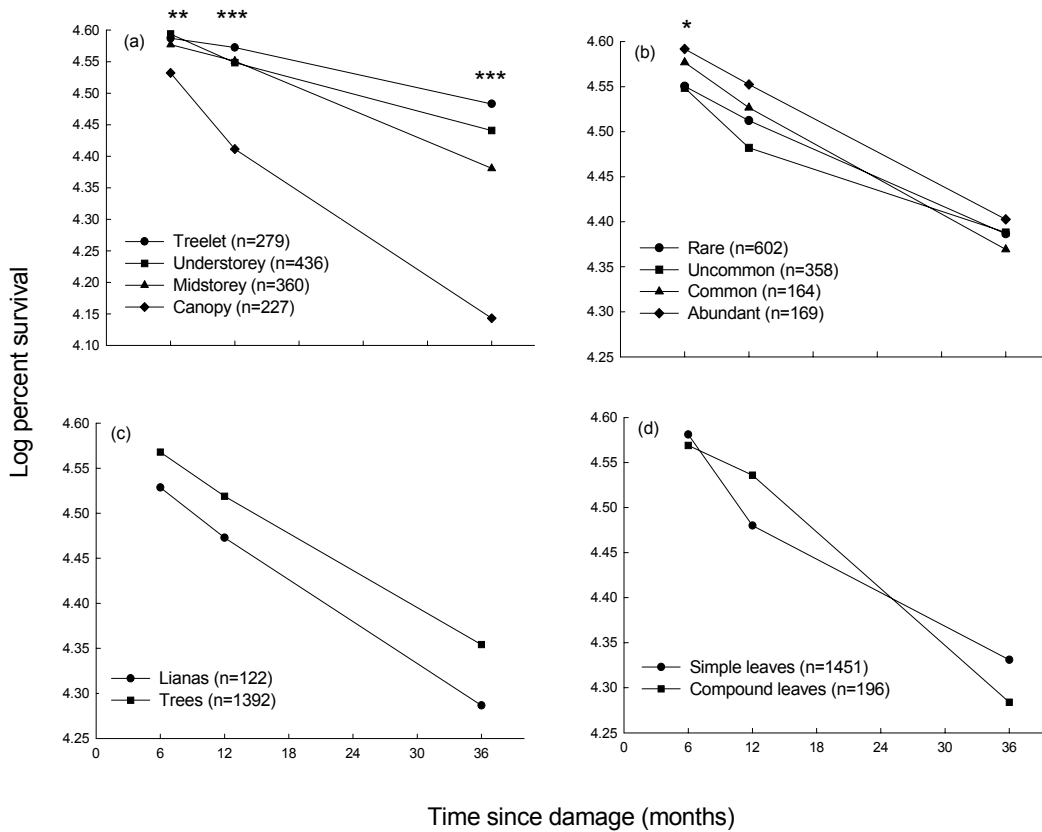


Figure 3.3 Log of percent survival after stem damage in relation to (a) strata at 6 ( $\chi^2 = 17.5$ ,  $df = 3$ ,  $P = 0.0006$ ), 12 ( $\chi^2 = 39.4$ ,  $df = 3$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 55.9$ ,  $df = 3$ ,  $P < 0.0001$ ), (b) abundance at 6 ( $\chi^2 = 12.5$ ,  $df = 3$ ,  $P = 0.006$ ), 12 ( $\chi^2 = 8.9$ ,  $df = 3$ ,  $P = 0.03$ ), and 36 months ( $\chi^2 = 0.7$ ,  $df = 3$ ,  $P = 0.88$ ), (c) habit at 6 ( $\chi^2 = 3.3$ ,  $df = 1$ ,  $P = 0.07$ ), 12 ( $\chi^2 = 2.2$ ,  $df = 1$ ,  $P = 0.14$ ), and 36 months ( $\chi^2 = 1.6$ ,  $df = 1$ ,  $P = 0.21$ ), and (d) leaf morphology at 6 ( $\chi^2 = 0.9$ ,  $df = 1$ ,  $P = 0.36$ ), 12 ( $\chi^2 = 5.0$ ,  $df = 1$ ,  $P = 0.03$ ), and 36 months ( $\chi^2 = 1.1$ ,  $df = 1$ ,  $P = 0.30$ ). \*  $P < 0.01$ , \*\*  $P < 0.001$ , \*\*\*  $P < 0.0001$ . Total sample sizes differed slightly among life history characteristics because it was not possible to categorize all stems for all characteristics.

(Fig. 3.3b). Neither growth habit (Fig. 3.3c) nor leaf morphology (Fig. 3.3d) was significantly related to survivorship at any time interval since damage.

### **Total shoot length (TSL)**

The summed length of all resprouting shoots on a given sapling (TSL) was used 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, and the correlation between BD and TSL increased up to 12 months (Fig. 3.4a,b,c). At 36 months the correlation was lower than at 12 months (Fig. 3.4d), perhaps as a consequence of other factors becoming more important (e.g., local light levels). Taller stumps also produced greater TSL at each time interval ( $R^2 = 0.12 - 0.22$ ;  $P < 0.0001$  for all times). 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 (data not shown).

Tree stratum was an important characteristic affecting TSL; species from higher strata produced greater TSL at all time intervals (Fig. 3.5a). Average TSL did not differ among abundance categories at any time interval (Fig. 3.5b). Trees and lianas produced similar TSL at 3 and 6 months, but trees produced greater TSL at 12 and 36 months (Fig. 3.5c). Simple-leaved plants had longer TSL at 6, 12, and 36 months but not at 3 months (Fig. 3.5d).

### **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  $2.4 \pm 0.1$ ). The number of new shoots was positively correlated with stump BD at all four time intervals (Fig. 3.6). The presence of leaves below the point of damage had no impact on the number of new shoots at any time interval (3 months  $\chi^2 = 1.5$ ,  $df = 1$ ,  $P = 0.22$ ; 6 months  $\chi^2 = 0.1$ ,  $df = 1$ ,  $P = 0.91$ ; 12 months  $\chi^2 = 0.1$ ,  $df = 1$ ,  $P = 0.71$ ; 36 months  $\chi^2 = 2.4$ ,  $df = 1$ ,  $P = 0.12$ )

The number of shoots produced was significantly different among strata; treelets had fewer shoots than larger strata at all times (Fig. 3.7a). This pattern mainly reflects morphological correlates of the growth form categories: treelets at PFR often are unbranched, so it is not unexpected that they produce only one new shoot after stem snap. Abundance was significantly related to number of shoots only at 36 months, when uncommon species had fewer shoots (Fig. 3.7b). Trees had more shoots than lianas at all times (Fig. 3.7c), and simple-leaved individuals always had more shoots than compound-leaved individuals (Fig. 3.7d).

### **Species-level responses**

The 13 most common species differed considerably in terms of survivorship, TSL, and number of new shoots (Table 3.1). There was no overall significant difference in survivorship among the 12 species tested between damaged stems and undamaged conspecific individuals ( $\chi^2 = 19.9$ ,  $df = 11$ ,  $P > 0.05$ ). *Chasalia curviflora* was not tested for survivorship because of identification ambiguity that was not clarified until 36 months, when potential conspecific individuals may have already died. The other species were readily identifiable in the field. *Shorea maxwelliana*, *Aporosa microstachya*,

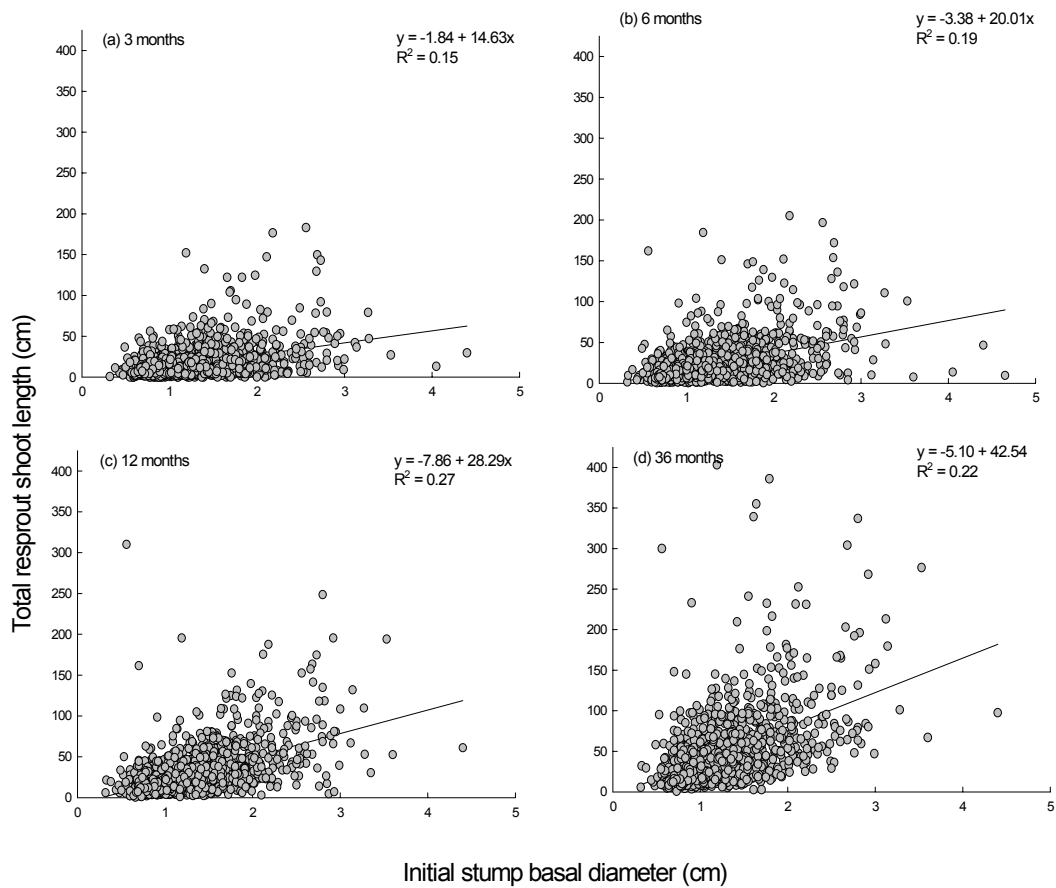


Figure 3.4 Scatter plots and regressions of total respout shoot length against initial stump basal diameter at (a) 3 months, (b) 6 months, (c) 12 months, and (d) 36 months at Pasoh Forest Reserve, Malaysia.

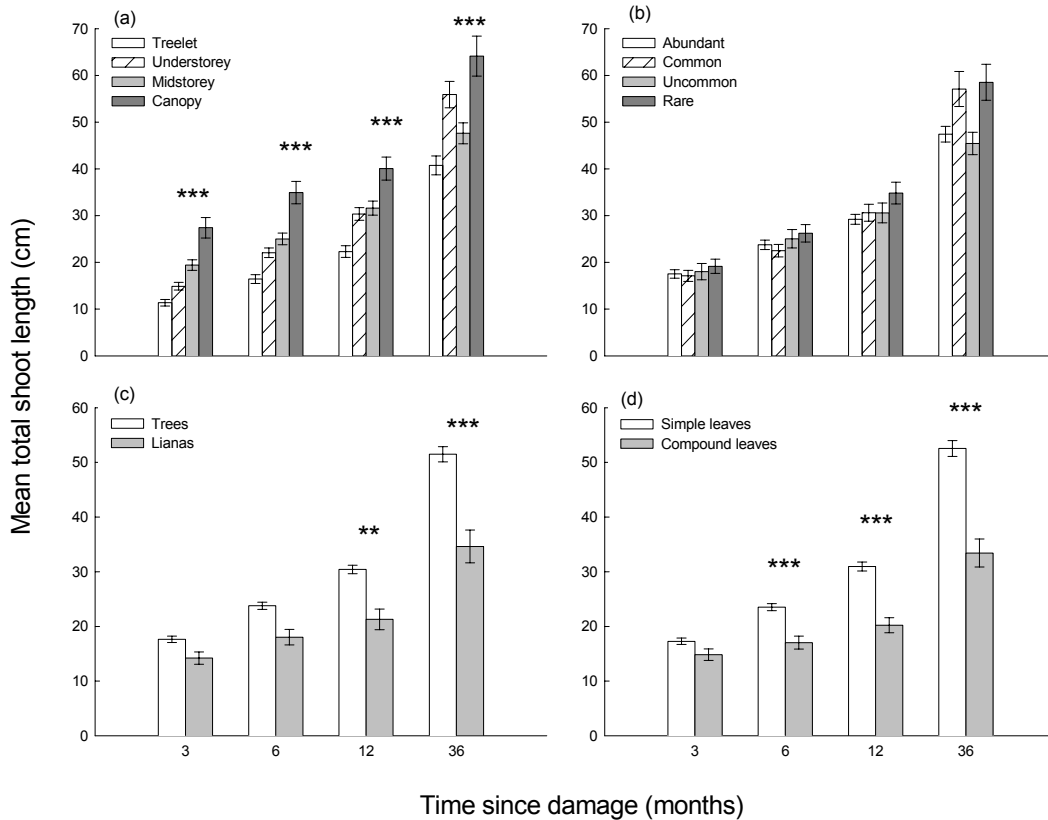


Figure 3.5 Mean total resprout shoot length per stump in relation to (a) strata at 3 ( $\chi^2 = 86.1$ ,  $df = 3$ ,  $P < 0.0001$ ), 6 ( $\chi^2 = 72.8$ ,  $df = 3$ ,  $P < 0.0001$ ), 12 ( $\chi^2 = 50.9$ ,  $df = 3$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 30.0$ ,  $df = 3$ ,  $P < 0.0001$ ), (b) abundance at 3 ( $\chi^2 = 3.9$ ,  $df = 3$ ,  $P = 0.28$ ), 6 ( $\chi^2 = 8.8$ ,  $df = 3$ ,  $P = 0.03$ ), 12 ( $\chi^2 = 8.7$ ,  $df = 3$ ,  $P = 0.03$ ), and 36 months ( $\chi^2 = 7.4$ ,  $df = 3$ ,  $P = 0.06$ ), (c) habit at 3 ( $\chi^2 = 0.3$ ,  $df = 1$ ,  $P = 0.58$ ), 6 ( $\chi^2 = 3.3$ ,  $df = 1$ ,  $P = 0.07$ ), 12 ( $\chi^2 = 11.3$ ,  $df = 1$ ,  $P = 0.008$ ), and 36 months ( $\chi^2 = 17.5$ ,  $df = 1$ ,  $P < 0.0001$ ), and (d) leaf morphology at 3 ( $\chi^2 = 0.4$ ,  $df = 1$ ,  $P = 0.55$ ), 6 ( $\chi^2 = 14.5$ ,  $df = 1$ ,  $P < 0.0001$ ), 12 ( $\chi^2 = 34.1$ ,  $df = 1$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 42.4$ ,  $df = 1$ ,  $P < 0.0001$ ). Kruskal-Wallis tests: \*  $P < 0.01$ , \*\*  $P < 0.001$ , \*\*\*  $P < 0.0001$ . Bars represent  $\pm 1$  SE. See Fig. 3 for sample sizes of each category.

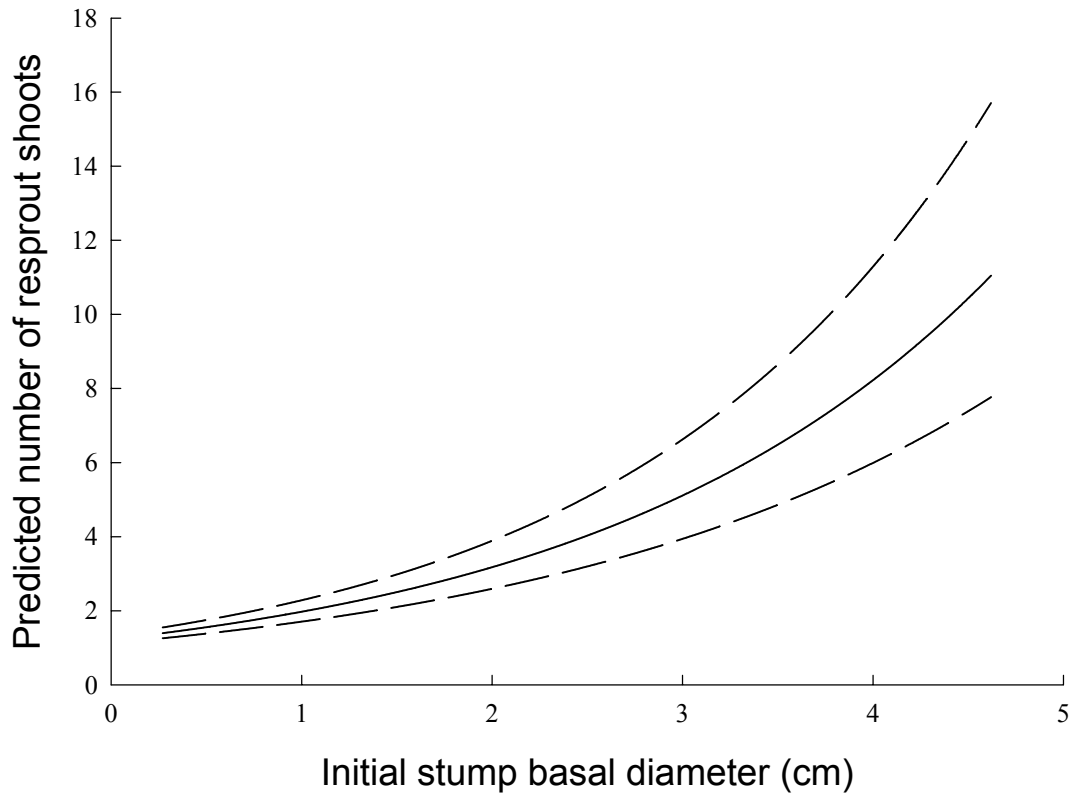


Figure 3.6 Predicted number of new shoots at 12 months based on stump basal diameter at time of stem damage ( $\chi^2 = 239.5$ ,  $df = 1$ ,  $P \leq 0.0001$ ). Dotted lines represent the Wald 95% confidence interval. Estimates of shoot number at 3, 6, and 36 months were quite similar to this curve (data not shown) and so are not pictured.

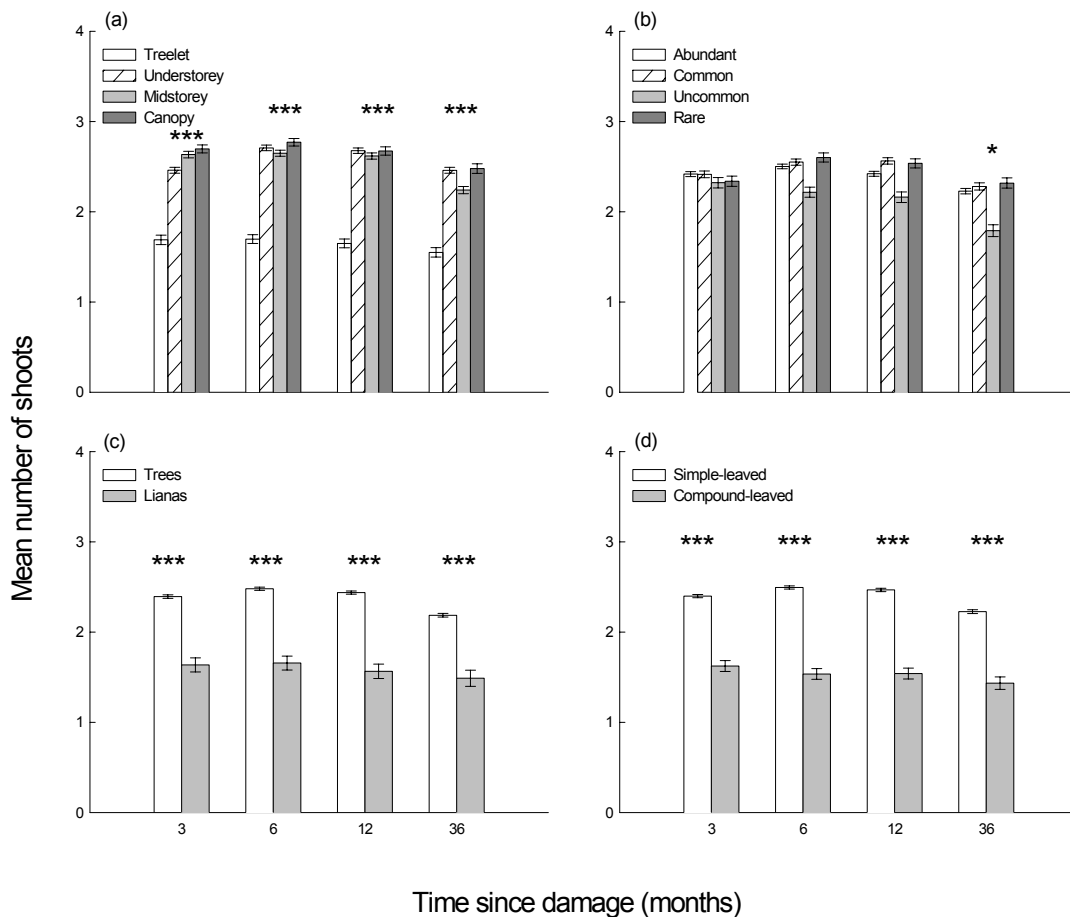


Figure 3.7 Mean number of resprout shoots in relation to (a) strata at 3 ( $\chi^2 = 64.5$ ,  $df = 3$ ,  $P < 0.0001$ ), 6 ( $\chi^2 = 88.8$ ,  $df = 3$ ,  $P < 0.0001$ ), 12 ( $\chi^2 = 89.9$ ,  $df = 3$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 66.6$ ,  $df = 3$ ,  $P \leq 0.0001$ ), (b) abundance at 3 ( $\chi^2 = 0.6$ ,  $df = 3$ ,  $P = 0.89$ ), 6 ( $\chi^2 = 5.7$ ,  $df = 3$ ,  $P = 0.13$ ), 12 ( $\chi^2 = 7.1$ ,  $df = 3$ ,  $P = 0.07$ ), and 36 months ( $\chi^2 = 12.3$ ,  $df = 3$ ,  $P = 0.006$ ), (c) habit at 3 ( $\chi^2 = 24.7$ ,  $df = 1$ ,  $P < 0.0001$ ), 6 ( $\chi^2 = 29.6$ ,  $df = 1$ ,  $P < 0.0001$ ), 12 ( $\chi^2 = 33.1$ ,  $df = 1$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 19.7$ ,  $df = 1$ ,  $P < 0.0001$ ), and (d) leaf morphology at 3 ( $\chi^2 = 42.7$ ,  $df = 1$ ,  $P < 0.0001$ ), 6 ( $\chi^2 = 70.8$ ,  $df = 1$ ,  $P < 0.0001$ ), 12 ( $\chi^2 = 63.2$ ,  $df = 1$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 41.7$ ,  $df = 1$ ,  $P < 0.0001$ ). Kruskal-Wallis tests: \*  $P < 0.01$ , \*\*  $P < 0.001$ , \*\*\*  $P < 0.0001$ . Bars represent  $\pm 1$  SE. See Fig. 3 for sample sizes of each category.

Table 3.1 Percent survival, mean 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. “N” represents the sample sizes for the different variables. Survivorship between damaged and undamaged conspecific saplings was tested with  $\chi^2$  analysis. \* P < 0.01, \*\* P < 0.001.

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

*Urophyllum hirsutum*, and *Xerospermum norhanianum* had significantly lower survivorship than undamaged conspecifics (Table 3.1).

Species-specific differences were observed in terms of TSL at all time intervals: 3 months ( $\chi^2 = 140.8$ ,  $df = 12$ ,  $P < 0.0001$ ), 6 months ( $\chi^2 = 187.1$ ,  $df = 12$ ,  $P < 0.0001$ ), 12 months ( $\chi^2 = 162.7$ ,  $df = 12$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 139.3$ ,  $df = 12$ ,  $P < 0.0001$ ). *Urophyllum hirsutum* and *Rinorea anguifera* resprouted prolifically, whereas *Rinorea horneri* and *Lepisanthes tetraphylla* produced little TSL (Table 3.1).

Number of shoots also differed at all time intervals: 3 months ( $\chi^2 = 145.6$ ,  $df = 12$ ,  $P < 0.0001$ ), 6 months ( $\chi^2 = 219.2$ ,  $df = 12$ ,  $P < 0.0001$ ), 12 months ( $\chi^2 = 204.0$ ,  $df = 12$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 176.1$ ,  $df = 12$ ,  $P < 0.0001$ ). *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 3.1).

### Family-level responses

Differences in resprouting were also found among the 19 families represented by 15 or more resprouting stems (Table 3.2). Among families overall, damaged individuals tended to have somewhat lower survivorship compared with undamaged individuals in the same family ( $\chi^2 = 31.9$ ,  $df = 18$ ,  $P = 0.02$ ). Stumps from the Dipterocarpaceae and Euphorbiaceae had especially low survivorship.

Families differed in terms of mean TSL at 3 months ( $\chi^2 = 166.2$ ,  $df = 18$ ,  $P < 0.0001$ ), 6 months ( $\chi^2 = 174.1$ ,  $df = 18$ ,  $P < 0.0001$ ), 12 months ( $\chi^2 = 152.5$ ,  $df = 18$ ,  $P < 0.0001$ ), and 36 months ( $\chi^2 = 100.4$ ,  $df = 18$ ,  $P < 0.0001$ ). Myrtaceae and Polygalaceae produced the highest mean TSL of the 19 families considered, while Connaraceae and Sapindaceae produced the least at 36 months (Table 3.2).

Number of resprout shoots also differed at all time intervals (3 months  $\chi^2 = 176.3$ ,  $df = 18$ ,  $P < 0.0001$ ; 6 months  $\chi^2 = 227.7$ ,  $df = 18$ ,  $P < 0.0001$ ; 12 months  $\chi^2 = 213.5$ ,  $df = 18$ ,  $P < 0.0001$ ; and 36 months  $\chi^2 = 180.1$ ,  $df = 18$ ,  $P < 0.0001$ ). 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 3.2).

### BD – DBH regression

Most studies of resprouting have examined larger trees and therefore used DBH, not BD, as the measurement of stem size. We were unable to measure DBH 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 DBH for a sample of  $> 7000$  stems at PFR (See Chapter II for methods). Basal diameter of 1.7 cm was equivalent to 1.0 cm DBH, and 3.0 cm BD corresponded to 2.0 cm DBH (K. Ickes unpubl. data). Consequently, 83% of stems in our study were  $< 1.0$  cm DBH prior to damage and virtually all were  $< 2.5$  cm DBH.

Table 3.2 Percent survival, mean 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 by only tree species; L indicates that the family was represented in the study by only liana species; and T/L indicates that both trees and lianas stumps were recorded. No. of species shows how many species comprise the categories damaged and undamaged stems for each family. “N” represents the sample sizes for the different variables. 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. \* P < 0.01 and \*\* P < 0.001.

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

## DISCUSSION

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 understory 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, survivorship at PFR was higher than that reported for trees after stem snap in Neotropical aseasonal rain forests. Only 27% resprouted in a Costa Rican cloud forest (Matelson *et al.* 1995), 41% resprouted in Amazonian Peru (Gorchov *et al.* 1993), and 51% of trees resprouted in lowland Panama (Putz *et al.* 1983).

### **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 similar tropical 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 only extended to 2.5 cm, whereas for the Neotropical studies “small” trees often included any tree < 15 cm DBH. The primary source of stem snap in these forests is branchfalls and treefalls, which Clark and Clark (1991) have shown damage more saplings 1 – 10 cm DBH than either larger or smaller stems. This pattern of litterfall damage may select for a bell-shaped response curve of DBH and resprouting ability, with the peak between 1 and 10 cm DBH. The broad diameter classes in the Neotropical studies (e.g., 1 - 15 cm DBH vs. > 15 cm) may mask this bell-shaped response curve. The Neotropical data and the data from our study suggest that in rain forests not prone to large-scale disturbance resprouting success is highest in stems 2.5 - 10 cm DBH.

Tropical forests that experience large-scale disturbance display different patterns in community-wide resprouting success. 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). In hurricane-prone tropical forests stem snap damage affects both small (from branchfalls and treefalls) and large (from hurricane winds) stems. Not surprisingly, resprout success in these forests is high for both small (< 15 cm DBH) and large (> 15 cm DBH) trees.

### **Do morphological and life history characteristics influence resprouting?**

If stem-damaging disturbance is sufficiently frequent, differential ability to survive and resprout subsequent to damage should influence the relative abundance of species in a given habitat: species less able to resprout should decrease in abundance as the frequency of disturbance increases (Knight 1975). Correlative evidence 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). However, survival data from PFR supported this hypothesis at only one of three time intervals: at 6 months abundant and common species had significantly greater survivorship than uncommon and rare species. There were no differences among abundance categories in TSL produced after damage, and only at 36 months were there significant differences in shoot number.

One mechanism to minimise 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 in Costa Rica 1 – 10 cm DBH experienced higher rates of stem damage from falling debris than either smaller or larger plants, and *within* the 1 – 10 cm DBH 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 DBH essentially “escape” the threat of stem snap by pigs, whereas treelet species always remain at risk. Guariguata (1998) qualified this “escape” hypothesis by noting that escape is an option only for species that grow to larger size classes; smaller species always face the threat of falling debris. 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, though differences in root-shoot partitioning, and the capacity to store and remobilise 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 remobilised 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. Given that liana species are generally light demanding (Schnitzer & Carson 2000; Schnitzer *et al.* 2000), an experiment investigating differential resprouting by growth habitat at various light levels might yield different results.

### **Are there differences in taxon-level survival or resprout vigor?**

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* 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 rubiaceous treelet. Similarly divergent resprouting responses were shown in shoot number and individual shoot length. *Chasalia* and *Rothmannia* produced on average  $< 1.4$  shoots/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/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 varied considerably at the family level as well. Dipterocarpaceae and Euphorbiaceae, the two dominant families with regard to stand structure and tree species richness in aseasonal forests of Southeast Asia, had especially poor stump survivorship. Dipterocarpaceae, the most important timber family in the region, accounts for  $> 24\%$  of the basal area at PFR and nine of the 10 most common emergent species. Euphorbiaceae is one of the most speciose families throughout Asian aseasonal lowland forests (Soepadmo 1995). In the 50-ha plot at PFR, the 87 euphorb species present comprise 11% of total tree species richness (Kochummen *et al.*, 1990).

### **Pigs and large scale edge effects**

As *Sus scrofa* is native to Peninsular Malaysia, nest building probably has 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 increasing an order of magnitude in recent decades (Ickes In press). 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 year-round food supply in the surrounding African oil palm plantations are edge effects that likely caused the increase. Pig density estimates were 27 – 47 individuals/km<sup>2</sup> from 1996 - 1998, and during this interval 560 pig nests/km<sup>2</sup>/year were constructed, producing  $> 85000$  stem snaps/km<sup>2</sup>/year (K. Ickes unpublished data). Pig density estimates and number of nests were conducted in the primary forest at the core of the reserve  $> 1.5$  km from the nearest forest margin. Pig density and number of nests are probably higher near the forest-palm plantation interface, but the high density at the core of the forest suggests that these edge effects are pervasive through the 2,500-ha reserve (Ickes and Williamson 2000). The scale of the edge effects results from the mobility of pigs.

The physical disturbance in the understory of PFR caused by nest building may substantially alter tree species composition in future generations. Given that pigs snap saplings without regard to species, changes in future species composition of the forest are likely to result from the differential ability of species to survive and resprout following damage. Perhaps the most pronounced change in Pasoh in response to increased pig densities will be a shift away from the currently dominant Dipterocarpaceae and Euphorbiaceae. The effects of pig nest building on tree regeneration, although falling outside of the usual typology of biotic interactions, are clearly of substantial importance in this system. PFR may be an extreme case,

but 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.

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## CHAPTER IV.

### EFFECTS OF NATIVE PIGS (*SUS SCROFA*) ON WOODY UNDERSTORY VEGETATION IN A MALAYSIAN LOWLAND RAIN FOREST: AN EXCLOSURE STUDY

This chapter has been published in *Journal of Tropical Ecology*, 17:191-206.

## INTRODUCTION

The influential role of vertebrate species in structuring plant communities is increasingly well documented. Medium to large bodied mammals can alter dynamics of plant species at population (Bergelson & Crawley 1992; Augustine & Frelich 1998) or community levels (McInnes *et al.* 1992; Schreiner *et al.* 1996), alter vegetation structure (McNaughton & Sabuni 1988) and species composition (Anderson & Loucks 1979), retard forest regeneration (Struhsaker *et al.* 1996), and decrease (Agnew *et al.* 1986; Virtanen *et al.* 1997) or increase richness (Guterman 1998). Significant effects on plant dynamics have resulted from grazing by lemmings (Virtanen *et al.* 1997), prairie dogs (Archer *et al.* 1987), and reindeer (Wegener & Odasz-Albrigtsen 1998); browsing by moose (Pastor *et al.* 1988) and elephants (Barnes *et al.* 1994); burrowing by pocket gophers (Huntly & Inouye 1988); dam building by beavers (Naiman *et al.* 1988); digging for subterranean food by grizzly bears (Tardiff & Stanford 1998), porcupines (Guterman 1982), and badgers (Platt 1975); seed predation by various species (De Steven & Putz 1984; Schupp 1988; Terborgh *et al.* 1993; Terborgh & Wright 1994; Blate *et al.* 1998); or trampling and mechanical damage (Plumptre 1993). The common or wild pig (*Sus scrofa*) exhibits several behaviors that may have dramatic influences on understory vegetation: soil rooting, nest building, and seed predation. Here we examine the extent to which this species alters plant communities, in this case the understory vegetation in a lowland rainforest in Malaysia.

*Sus scrofa* has a natural geographical range that extends throughout Europe and Asia as far south and east as the Malay Peninsula and the islands of Sumatra and Java. The species occupies a diversity of habitat and vegetation types. *Sus scrofa* has also been introduced in numerous locations outside their native ranges and populations are currently well established in New Zealand (Caughley 1970), Australia (Hone 1990), North America (Singer 1981), Hawaii (Stone & Loope 1987), the Galapagos (Coblentz & Baber 1987), and numerous other islands (Challies 1975; Baron 1982; Baber & Coblentz 1986). Although *S. scrofa* is known to have detrimental effects on forest communities where introduced, little is known about its impact on communities to which they are native.

*Sus scrofa* is an omnivorous species, so diets vary greatly among habitats and geographic locations (Henry & Conley 1972; Diong 1973; Klaa 1992). In all areas, however, large proportions of their diets are subterranean in origin and the animals regularly root through soil (Genov 1981; Singer 1981). Rooting may affect vegetation directly by displacing and killing seedlings or indirectly by altering physical properties of the soil, changing nutrient dynamics (Lacki & Lancia 1983; Singer *et al.* 1984), or facilitating the spread of exotic vegetation (Aplet *et al.* 1991).

Another aspect of their diet that may alter the plant community is frugivory and subsequent seed mortality. Throughout their range, pigs are known to eat large quantities of fruits and seeds when available. In the Sunda Shelf region of Southeast Asia, mast fruiting occurs on a supra-annual scale for many plant species (Whitmore 1984). One hypothesis for fruiting synchrony is predator satiation during fruiting events (Kelly 1994). Wild (*S. scrofa*) and Bearded pigs (*S. barbatus*) are thought to be two of the most important predators of fallen fruits and seeds. Thus, seed predation by pigs may, in large part, account for the mast fruiting phenomenon in southeast Asia (Curran and Webb 2000; Curran and Leighton 2000).

Nest-building is yet another behavior of pigs that may influence plant dynamics. Prior to giving birth, female pigs generally gather vegetation into a pile and deliver their young beneath. In primary lowland rain forest of Peninsular Malaysia, pigs form nests primarily from woody

tree saplings 40-350 cm in length that they uproot or snap off. As a single nest may comprise over 500 stems, nest-building may reduce stem density and increase plant mortality dramatically at a local scale (K. Ickes, unpubl. data).

We quantified the impacts that *S. scrofa* has on understory plant density and diversity in primary, lowland rain forest in Peninsular Malaysia. In experimental plots we removed the possible influences on plants of pig rooting, nest building, and frugivory. We predicted that excluding pigs would lead to increases in woody plant recruitment, stem density, species diversity, and growth. In addition, we predicted that the proportion of woody stems made up of lianas, as well as overall plant mortality, would decrease within exclosures.

## MATERIALS AND METHODS

### Study system

This study was conducted in Pasoh Forest Reserve (PFR), which lies 110 km southeast of Kuala Lumpur in the state of Negeri Sembilan, Malay Peninsula (2° 59' N, 102° 18' E). The reserve comprises a core area of 650 ha of primary lowland dipterocarp forest and a 650 ha buffer zone of selectively logged lowland forest regenerating from logging that occurred 40 years ago. Another 650 – 1,000 ha of primary hill dipterocarp forest comprise the eastern portion of the reserve. Aside from a corridor of hill forest that connects PFR to the southern end of the main mountain range, the remaining perimeter (approximately 85%) is bordered by mature African oil palm (*Elaeis guineensis* Jacq.) plantations. The flora of PFR is exceptionally diverse, with high liana diversity (Appanah *et al.* 1993) and over 800 tree species  $\geq 1.0$  cm DBH (diameter at breast height) recorded in a 50-ha tree plot (Kochummen 1997). Annual rainfall is approximately 2,000 mm with a known range of 1700 – 3200 (Kochummen *et al.* 1990). Monthly rainfall means exceed 100 mm, providing an aseasonal climate.

### Exclosure design

Exclosures were constructed between 30 June and 11 July 1996 in primary forest south of the permanent, 50-ha study plot. Beginning at the origin of this plot, an exclosure was constructed 40 meters to the south, and at subsequent 40-meter intervals eastward. Exclosures consisted of a 7 x 7 x 1.5 m chain-link fence with 4-cm<sup>2</sup> mesh. Dense wood (probably *Neobalanocarpus heimii*) was used for the four corner posts and two supporting posts/edge. Post holes were dug to a depth of roughly 50 cm, the chain-length fence nailed to the wood, with the bottom pressed firmly against the ground. To ensure that pigs did not root under the fence, up to four rows of barbed wire encircled each fence, from ground level to 60 cm in height. Exclosures were open above. Because of this open-top design and the wide mesh size, it did not appear that the exclosures altered light, wind speed, rainfall, or other microclimate conditions.

Two control plots were paired with each exclosure in a randomized block design. These were placed one meter outside of the exclosures on two of the four sides. Control plots were placed subjectively on the two sides that most closely resembled the vegetation structure within the paired experimental plot. A 5 x 5 m plot, centered within each exclosure and each control area, was delineated with small PVC pipes placed at the corners, driven deep into the soil to reduce visibility to pigs.

### **Vegetation sampling**

For the initial survey, plants were measured between 12 August and 21 September 1996. Within experimental ( $n = 8$ ) and control ( $n = 16$ ) plots, all woody, free-standing plants  $\geq 30$  cm height were identified, mapped, and measured for basal diameter, DBH (if applicable), and height up to 740 cm using a telescoping measuring pole. Freestanding lianas were included in the survey. Plants were tagged within the exclosures. Because pigs are known to chew aluminum tags, plants in the controls were carefully mapped but not tagged. We encountered no difficulty in relocating the plants for subsequent measurements.

The second survey took place from 1 - 20 August 1998. We recorded the same measurements or noted mortality, and all new plants that had recruited into the  $\geq 30$  cm height category were added (hereafter called recruits). Seventeen plants were found in 1998 that were not considered to be recruits because they were obviously present, but missed, during the 1996 survey. Additionally, in 1998 only, all seedlings of woody plants  $< 30$  cm tall were counted but not identified in 1 x 1 m plots in the corners of the 5 x 5 m study plots (hereafter called seedlings). By working close to the edges of the plots, we were able to survey these subplots without trampling the seedlings.

Plant species were identified by K. Ickes, primarily based on prior identification of species for the 50-ha permanent plot at Pasoh. Unknown species were collected and identified at the herbarium of the Forestry Research Institute of Malaysia with assistance from herbarium staff and visiting specialists.

### **Mast-fruiting at PFR**

Mast fruiting occurred in 1983, 1990, and 1996 at PFR, although very little fruit fell before completion of the fences on 11 July 1996. Prior to completion of the vegetation sampling on 21 September 1996, however, most fruits had fallen and many had begun to germinate, creating a dense seedling carpet in some areas. Attempts were made to minimize damage to small plants while surveying vegetation plots. Despite the daily increase in the number of seedlings, we feel that there was little or no bias in surveyor-caused mortality of seedlings among plots, as the last plot to be surveyed in 1996 had the second highest number of recruits in 1998. In addition, none of the new seedlings from the mast event were included in 1996, even in the last plots surveyed, because they were not tall enough ( $\geq 30$  cm) at the time of the survey.

### **Data analysis**

Statistical analyses were conducted using SAS version 6.12 (SAS Institute 1997). Data with non-normally distributed residuals were log transformed. Several variables did show deviations from normality, even after transformations. While ANOVA is a robust analysis and can tolerate even substantial deviations from normality, p-values should be judged accordingly. Using PROC MIXED, we tested the effect of treatment (exclosure vs. control) on recruitment, mortality, growth, seedling number, overall stem density, stem density within different size classes, proportion of stems between 30 - 100 cm tall made up of lianas, species richness, and Fisher's log series  $\alpha$ . Treatment was a fixed effect and block ( $n = 8$ ) was a random effect in all ANOVAs. For variables measured in both years the 1996 values were used as covariates. In addition, for recruitment and mortality the number of stems in 1996 was used as a covariate. For growth, the height of trees in 1996 was used as a covariate. The number of individuals in the four seedling sub-plots was combined for plot comparisons.

Growth was determined as the difference in height between 1998 and 1996. Growth was compared for trees initially between 1 – 7 m tall, trees initially between 30 - 100 cm tall, and lianas initially 30 - 100 cm in height. In addition, we tested species-specific growth responses to pig exclusion in the eight species that had more than 50 stems survive from 1996 to 1998.

Changes in diversity were examined in two ways: number of species and Fisher's log series  $\alpha$  index. For Fisher's  $\alpha$ , values of the  $x$  parameter were calculated in SAS using a simple iterative program. Only individuals for which species level identifications or morphotypes had been made were included in the diversity analyses. Therefore, 139 stems (5.67 % of total) were removed from the 1996 calculations and 132 stems (4.63 % of total) from the 1998 calculations. Species richness values are thus underestimated because many of the unidentified individuals represent rare species.

Survival as a function of height in the control vs. exclosure plots was analyzed by logistic regression with a Bernoulli (binary) distribution and a logit link (PROC GENMOD).

## RESULTS

The 1996 survey of freestanding stems  $\geq 30$  cm tall consisted of 2,452 individuals and 278 species (including 33 morphospecies). Species and family dominance were low in the study area, the most common species *Xerospermum norhanianum* accounting for only 4.3% of the total number of stems, and only 5.2% of stems between 30 and 50 cm tall (Table 4.1). The lianas *Caesalpinia parviflora* and Morphotype 1 (Connaraceae) may be the most common woody plants in the study area, as we only recorded their freestanding stems. Lianas composed 490 (26%) of the 1,962 stems between 30 and 200 cm tall. Between 1996 and 1998, 229 plants died and 629 stems recruited into the  $\geq 30$  cm size class. Species dominance was much higher among recruits than among plants from the 1996 survey, with the most abundant species comprising 21.8% and the three most abundant accounting for 53.3% of all recruits (Table 4.1).

After two years, no differences were found in mortality between experimental and control plots (Fig. 4.1). Tall plants had significantly higher odds of survival than shorter plants ( $\chi^2 = 11.21$ ,  $P < 0.001$ ), but the odds of survival did not differ between exclosures and controls ( $\chi^2 = 0.36$ ,  $P = 0.55$ ). In contrast to mortality, the number of recruits in exclosures was three times greater than the number in controls (Fig. 4.1). Seven out of eight exclosures had higher recruitment than their paired control plots, while the eighth exclosure had more recruits than one of its two paired controls. Recruits in exclosures were also slightly taller than recruits in controls (Table 4.2). Seedling (untagged plants  $< 30$  cm tall) plots within fences had 56% more individuals in 1998 than controls (Table 4.2). Given the lack of mortality differences but significant recruitment differences, woody stem density in 1998 was much higher in exclosures ( $142.3 / \text{m}^2$ ) than in controls ( $107 / \text{m}^2$ ) (Table 4.2). This difference was the result of large increases in the number of stems in the two smallest size categories: 30 – 40 and 40 – 50 cm tall (Fig. 4.2).

Species diversity in 1998, as measured by Fisher's  $\alpha$ , was significantly lower in exclosures than in controls (Table 4.2). Number of species, however, was greater within exclosures (Fig. 4.3). Number of stems and number of species in 1998 were highly correlated in both exclosures ( $R^2 = 0.73$ ) and controls ( $R^2 = 0.82$ ). This relationship did not differ for control and exclosure plots in the 1996 survey (ANCOVA,  $F = 0.36$ ;  $df = 3, 23$ ;  $P = 0.56$ ), but was significantly different in 1998 (ANCOVA,  $F = 6.44$ ;  $df = 3, 23$ ;  $P = 0.02$ ); more species

Table 4.1 Ten most common species from the initial survey in 1996 and eight most common species that recruited into the  $\geq 30$  cm size class between 1996 and 1998. Number of stems includes individuals from all size classes, whereas number of small stems includes only plants between 30 and 50 cm tall. *Caesalpinia*, the three dipterocarp species, and *Alchornea* all had tremendous fruit crops during the mast fruiting of 1996; *Rinorea horneri* probably fruited continuously; and *Willughbeia* had a large fruit crop immediately prior to the 1998 survey. We have no information about the phenology of Morphotype 1 from the Connaraceae.

Species	Family	Habit	No. stems	Cum. % total stems	No. small stems	Cum. % small stems
<b>1996 Survey</b>						
<i>Xerospermum norhanianum</i> Bl.	Sapindaceae	Tree	105	4.3	53	5.2
<i>Anaxagorea javanica</i> Bl.	Annonaceae	Tree	82	7.6	46	9.8
<i>Shorea maxwelliana</i> King	Dipterocarpaceae	Tree	80	10.9	29	12.7
<i>Caesalpinia parviflora</i> Prain ex King	Leguminosae	Liana	68	13.7	51	17.7
<i>Ardisia crassa</i> C.B. Clarke	Myrsinaceae	Tree	63	16.2	26	20.3
<i>Rothmania macrophylla</i> (Hk. F.) Bremek.	Rubiaceae	Tree	63	18.8	28	23.0
Morphotype 1	Connaraceae	Liana	55	21.0	31	10.8
<i>Rinorea horneri</i> (Korth.) O.K.	Violaceae	Tree	55	23.3	27	28.8
<i>Shorea macroptera</i> Dyer	Dipterocarpaceae	Tree	37	24.8	9	29.7
<i>Leptonychia glabra</i> Turcz.	Sterculiaceae	Tree	35	26.2	9	30.6
<b>1998 Recruits</b>						
<i>Caesalpinia parviflora</i> Prain ex King	Leguminosae	Liana	137	21.8		
<i>Shorea leprosula</i> Miq.	Dipterocarpaceae	Tree	126	41.8		
<i>Shorea macroptera</i> Dyer	Dipterocarpaceae	Tree	72	53.3		
<i>Willughbeia coriacea</i> Wall.	Apocynaceae	Liana	27	57.6		
<i>Rinorea horneri</i> (Korth.) O.K.	Violaceae	Tree	18	60.4		
<i>Dipterocarpus costulatus</i> V. Sl.	Dipterocarpaceae	Tree	16	63.0		
Morphotype 1	Connaraceae	Liana	11	64.7		
<i>Alchornea rugosa</i> (Lour.) M.A.	Euphorbiaceae	Tree	10	66.3		

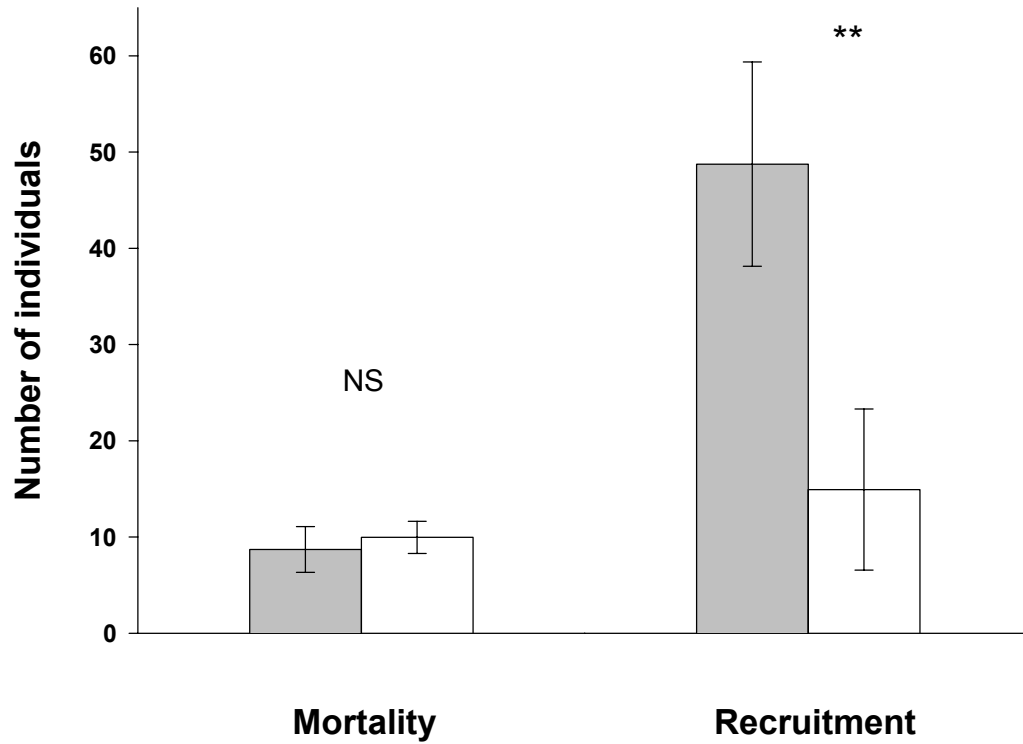


Figure 4.1 Mean mortality and number of individuals that recruited into the  $\geq 30$  cm tall size class for enclosures ( $n = 8$ ) vs. controls ( $n = 16$ ). All values are LS Means calculated in SAS using PROC MIXED with the number of stems in 1996 used as a covariate.

Table 4.2 Results of ANOVA tests for treatment effects. Average values are LS Means calculated in SAS using PROC MIXED. All variables had a covariate in the ANOVA except height of recruits, number of seedlings, and proportion of recruits made up of lianas. For growth rates of the eight species with  $\geq 50$  stems surviving between surveys, plants that lost more than 10 cm of stem height were deleted from the analyses (17 total), as was one extreme positive growth outlier for each of three species. The final sample sizes for growth under each treatment are shown in parentheses after the standard errors. Degrees of freedom differ according to the number of plots in which the species was found.

Variable	LSMeans $\pm$ S.E.		df	F	P > F
	Exclosure	Control			
<b>Stand Structure</b>					
Mortality 1996-1998	8.7 $\pm$ 2.37	10.0 $\pm$ 1.67	1, 14	0.48	0.50
Recruits (> 30 cm tall) 1996-1998	48.8 $\pm$ 10.6	14.9 $\pm$ 8.4	1, 14	10.61	0.006
Height of recruits (cm) 1996-1998	36.1 $\pm$ 0.72	34.5 $\pm$ 0.59	1, 15	4.78	0.05
Seedlings (< 30 cm tall) 1998	117.5 $\pm$ 21.0	75.5 $\pm$ 17.8	1, 15	4.84	0.04
Stem density 1998	142.3 $\pm$ 11.3	107.1 $\pm$ 8.4	1, 14	9.26	0.009
<b>Species Diversity</b>					
Species richness 1998	55.7 $\pm$ 1.05	50.6 $\pm$ 1.06	1, 14	7.24	0.02
Fisher's $\alpha$ 1998	39.7 $\pm$ 2.81	45.8 $\pm$ 2.31	1, 14	5.48	0.04
<b>Lianas</b>					
Liana proportion of stems 30 - 100 cm tall 1998	30.5 $\pm$ 2.6	25.9 $\pm$ 2.0	1, 14	2.9	0.11
Liana proportion of recruits 1996-1998	36.2 $\pm$ 9.0	31.7 $\pm$ 7.7	1, 15	0.31	0.58
<b>Height Growth (cm) 1996-1998</b>					
Trees initially 101 - 700 cm tall	19.64 $\pm$ 3.04	12.88 $\pm$ 2.41	1, 15	4.85	0.04
Trees initially 30 - 100 cm tall	10.09 $\pm$ 1.39	8.23 $\pm$ 1.11	1, 15	1.36	0.22
Lianas initially 30 - 100 cm tall	9.69 $\pm$ 2.36	9.69 $\pm$ 1.84	1, 15	0	1.00
<b>Eight most common species 1996-1998</b>					
<i>Xerospermum norhanianum</i> Bl.	6.75 $\pm$ 1.34 (32)	6.88 $\pm$ 1.09 (52)	1, 11	0.01	0.94
<i>Anaxagorea javanica</i> Bl.	13.18 $\pm$ 1.97 (25)	10.33 $\pm$ 1.44 (51)	1, 6	1.56	0.26
<i>Shorea maxwelliana</i> King	32.10 $\pm$ 3.97 (17)	13.12 $\pm$ 4.67 (53)	1, 8	5.09	0.05
<i>Caesalpinia parviflora</i> Prain ex King	11.25 $\pm$ 2.59 (20)	5.58 $\pm$ 1.59 (39)	1, 5	5.68	0.06
<i>Ardisia crassa</i> C.B. Clarke	5.45 $\pm$ 1.84 (13)	8.14 $\pm$ 1.11 (36)	1, 5	1.57	0.27
<i>Rothmania macrophylla</i> (Hk. F.) Bremek.	11.32 $\pm$ 2.48 (38)	7.49 $\pm$ 2.27 (20)	1, 9	1.3	0.28
Morphotype 1	7.56 $\pm$ 1.93 (15)	3.83 $\pm$ 1.44 (33)	1, 11	3.2	0.10
<i>Rinorea horneri</i> (Korth.) O.K.	6.10 $\pm$ 1.85 (13)	6.62 $\pm$ 1.28 (39)	1, 6	0.07	0.80

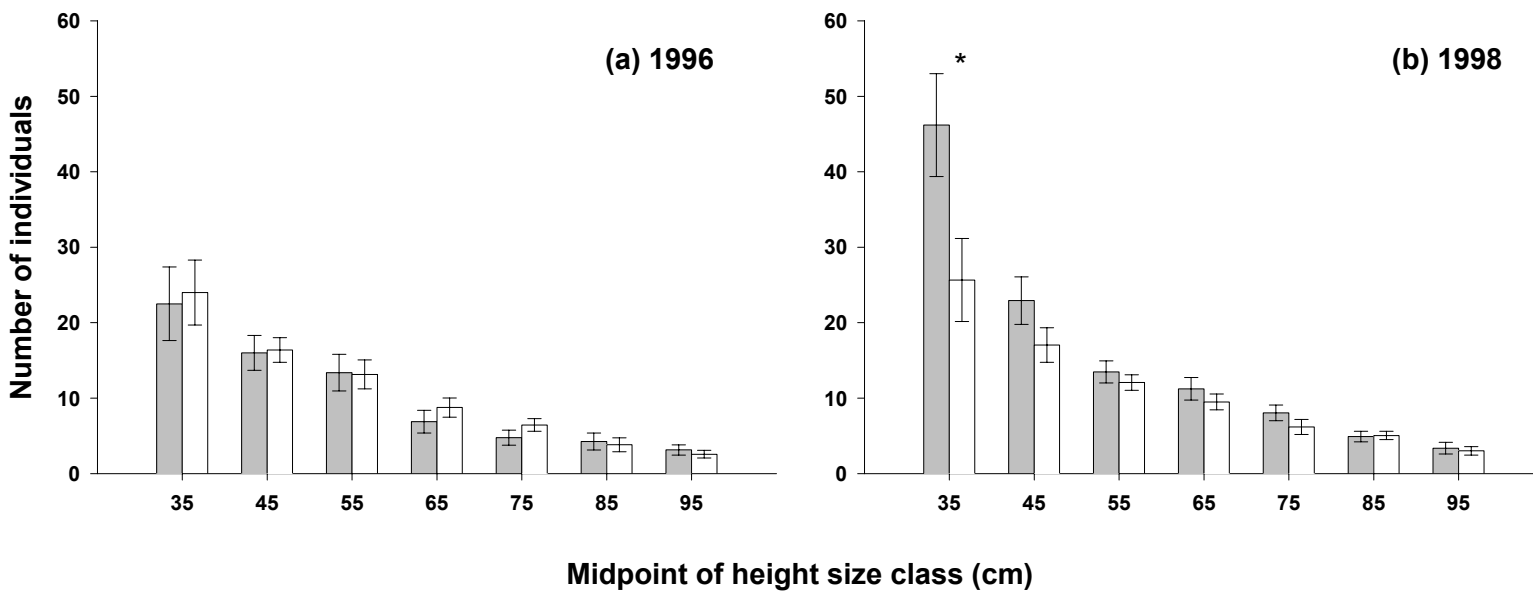


Figure 4.2 Height size class histograms of 10 cm increments for plants < 100 cm tall in controls and exclosures from 1996 and 1998. Height classes are represented by the increment midpoint (i.e. 35 represents the height increment from 30 – 39 cm tall). Number of individuals in the exclosures is the total number of plants in all exclosure plots (n=8) in a given size class. Number of individuals in the controls is the total number of plants in all control plots (n=16) in a given size class divided by two to standardize for area.

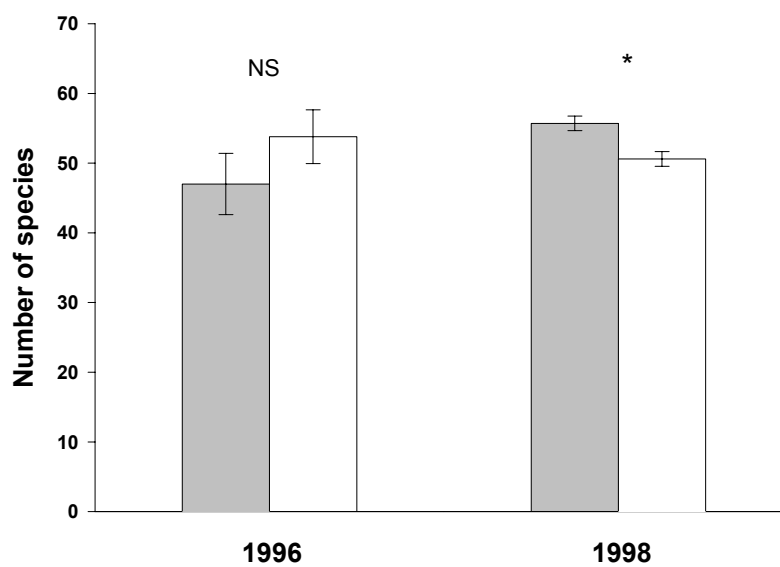


Figure 4.3 Average species richness values for exclosures (n = 8) and controls (n = 16) in 1996 and 1998. The 1998 values are LS Means calculated in SAS using PROC MIXED with 1996 values used as a covariate.

accumulated per individual stem in controls ( $y = 18.60 + 0.33x$ ) than in exclosures ( $y = 27.74 + 0.18x$ ).

Overall height growth of stems initially between 1 – 7 m tall was 50% greater inside exclosures (Table 4.2). No differences were found for trees initially 30 - 100 cm tall. Of the eight most common species surviving between surveys, three showed marginally significant greater mean height growth in exclosures (Table 4.2). The other five most common species had similar mean growth increments in each treatment.

No treatment differences were detected in height growth for freestanding lianas initially 30 – 100 cm tall (Table 4.2). No significant differences were found in the proportions of stems between 30 and 100 cm tall made up by lianas. Nor were differences in liana proportions found among the recruits (Table 4.2).

## DISCUSSION

### Exclusion of vertebrates

Due to the wide mesh size of the fence and open top design, we assumed that all birds, rodents, civets (several of which are partially frugivorous), and primates could readily enter the exclosures. Consequently, the only potential vertebrate seed predators or herbivores excluded were large terrestrial mammals. Lowland rain forests in Peninsular Malaysia historically contained a number of medium to very large terrestrial herbivores. Indian elephant (*Elephas maximus*), Malayan tapir (*Tapirus indicus*), Javan rhinoceros (*Rhinoceros sondaicus*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*), greater mouse-deer (*Tragulus napu*), lesser mouse-deer (*T. javanicus*), Malayan porcupine (*Hystrix brachyura*), brush-tailed porcupine (*Atherurus macrourus*), wild pig (*Sus scrofa*), and bearded pig (*S. barbatus*) all probably occurred at PFR until this century and some until quite recently (Medway 1983). Currently, however, most of these species are extinct or rare within PFR because of the small reserve size, relatively homogenous habitat within the remaining area, poaching, habitat fragmentation in the surrounding area, relative isolation, and removal of potentially dangerous animals from the surrounding oil palm tree plantations by the Wildlife Department. Therefore, the only herbivores excluded during this study were the focal organism, *S. scrofa*, both porcupine species, and the lesser mouse-deer. Lesser mouse-deer are common at PFR, but are not as common as pigs (K. Ickes, *pers. obs.*), and mouse-deer neither build nests for reproduction nor disturb soil by digging. Both porcupines are still present at Pasoh but at apparently low densities; only one individual porcupine was seen during > 250 hours walking line transects at dusk and dawn, compared with hundreds of wild pigs (K. Ickes, unpubl. data).

### Nest building

The net effect of pig exclusion on the understory vegetation at Pasoh Forest Reserve was considerable. After two years in the absence of pigs, the average size of recruits, number of recruits, overall stem density, and species richness were all greater inside exclosures than in paired controls. The exclosures were designed to eliminate all pig activity including nest building, rooting, and seed predation. However, the differences found between exclosures and controls are not likely due to nest building. During the two years of this study, only one nest was built in the research area, about 2 m away from one of the controls. Mortality in that control plot was almost twice that of any other plot, but the overall mortality rate between treatments still did not differ significantly. In addition to high mortality in that plot, 22 plants near the nest had

negative height growth rates, and at least 12 of these had stems snapped off by a pig for nest construction. Nonetheless, four other plots had similar or higher numbers of stems with negative growth due to factors other than pigs (e.g., plants damaged by branchfall or stem borers). Consequently, nest building appears to have caused little, if any, of the observed differences in the understory vegetation between treatments. We therefore attribute the differences in this enclosure study to pig rooting and seed predation. Whether differences are due more to rooting or seed predation is, impossible to determine here.

### **Seed predation**

Vertebrate seed predation has been shown to decrease seed survivorship dramatically in other tropical forests and likely is an important factor affecting plant dynamics at PFR. In a dipterocarp forest of Borneo, Blate *et al.* (1998) report that after only 30 days, more than 50% of seeds experimentally placed in transects suffered mortality due to predation. In Panama, De Steven and Putz (1984) documented intense but variable seed predation within a year for *Dipteryx panamensis*; at three different sites, 36, 97, and 98% of seeds were eaten by vertebrates.

Although no other enclosure experiments have been published from tropical Southeast Asia, the results reported here are comparable to those of several enclosure studies from the Neotropics. Terborgh and Wright (1994) conducted a comparative study of vertebrate exclusion between two lowland rainforest sites, Barro Colorado Island (BCI) in Panama and Manu in Peru. They experimentally placed seeds inside enclosures and in adjacent controls, and found that 36 and 3% survived in Peru, respectively (counting missing seeds from controls as dead). The results were similar in Panama, where 25% of the seeds survived inside enclosures but none survived in controls. As with our study, they documented no differences in seedling mortality between enclosures and controls, but recruitment was significantly greater in controls. The results of our study are also consistent with those from another, current study utilizing large, permanent enclosures on BCI and the adjacent mainland. Excluding seed and seedling predators has led to dramatic increases in seedling recruitment, stem density, growth, and species richness (W. Carson *pers. comm.*). *Sus scrofa* is known to consume large quantities of seeds when available in other areas (Henry & Conley 1972; Klau 1992), and probably is an important seed predator in Malaysia as well. In our study, it seems likely that seed predation by pigs can account, to some extent, for the lower number of recruits and seedlings < 30 cm tall in control plots.

### **Soil rooting**

Pig rooting may also influence understory plant density and diversity and account to some extent for the findings of this study. In Great Smoky Mountains National Park (GSMNP) in the southeastern United States, rooting by introduced pigs was shown to decrease herbaceous ground cover from approximately 90 to 10 % (Bratton 1975), alter species composition in favor of those with deep or poisonous roots, decrease plant species richness (Bratton 1974), and virtually eliminate two leaf-litter-dependent vertebrates (Singer *et al.* 1984). As there is little herbaceous vegetation at PFR, the decreases in woody seedling density reported here from Malaysia may be comparable to decreases in herbaceous ground cover in the continental USA. Herbaceous cover in the GSMNP returned to normal levels three years after pig enclosures were built, but species richness remained lower than expected (Bratton *et al.* 1982). Mean species richness per plot increased over two years in our enclosures while staying roughly the same in controls. Diversity as measured by Fisher's  $\alpha$ , however, was higher in control plots. These seemingly contrasting

results may be a function of the significant increase in stem density within exclosures without a concomitant increase in new species. On average in 1996, one new species was measured for every three stems, while in 1998 one was measured only for every five stems. In addition, the species richness increase within exclosures can be attributed to the increase in stem density, not to an overall gain in species number; cumulative species richness across plots in 1998 was identical between exclosures and controls. Furthermore, the large increase seen in the number of plants in the two smallest size classes suggests that pigs at Pasoh Forest Reserve are having an unusually strong influence on understory plant dynamics. As seen in Figure 4.2, the size class histograms for exclosures in 1998 represent a more typical distribution of plants across increasing size classes, in which there is an abundance of small seedlings; the same size categories for controls in 1998 and both categories in 1996 show uncharacteristically linear decreases in stem density in size classes of increasing height (Richards 1996).

In addition to changes in cover and composition, pig rooting may also affect plant growth rates. Lacki and Lancia (1986) found that the dominant overstory tree species in GSMNP, *Fagus grandifolia*, showed increased shoot elongation in areas rooted by pigs. The increase was hypothesized to result from an increase in humus breakdown rates and more aeration of soils in pig-rooted areas. In this study, a difference was found in overall height growth for trees initially between 1 – 7 m tall in rooted vs. un-rooted plots, but plants in exclosures grew more. Similar results were seen at the species level. Of the eight species with  $\geq 50$  individuals surviving from 1996 to 1998, three had marginally greater ( $P \leq 0.10$ ) height growth in the exclosure plots (Table 4.2). These data are in contrast with the positive effects of pig rooting on growth rates for *Fagus grandifolia*. Pig rooting, however, may have different impacts on different species. Response differences may depend on variables such as tree size, root growth patterns, and mycorrhizal associations. Also, Lacki and Lancia measured shoot elongation in large trees of a species poor forest. Our study, in contrast, measured height growth in understory plants in an exceptionally diverse area. Finally, it should be noted that the mean growth rates were quite low in the Malaysian understory. It is possible that growth responses to pig exclusion are stronger than documented here, but that more than two years are needed to detect such differences in understory conditions.

Pig rooting may also induce plant mortality, but in a manner unable to be detected with our experimental design. All susceptible individuals might have already died prior to our initial survey because pigs seem to root the same areas repeatedly at PFR and may have been doing so for years. Even if such rooting kills seedlings and saplings, as seems likely, no differences in mortality between treatment and control plots would have been detected, thereby giving the false result that rooting does not kill plants directly. Roughly half of the control plots appeared to be thoroughly disturbed by rooting in 1996. Consequently, we would only have detected impacts of rooting on seedling mortality where pigs rooted previously undisturbed control plots.

The impacts of rooting which predated this study might be sufficiently long lasting as to underestimate the effects of pigs. Rooting-induced alterations to seedling regeneration niches (sensu Grubb 1977) might require more than two years to return to pre-rooted levels. For example, the exclosure area in plot 1 was heavily disturbed prior to fencing in 1996. In early October 1996, following the mast fruit fall and seed germination, there were perhaps 500-800 seedlings in the exclosure plot but less than 20 in each paired control (Ickes, *pers. obs.*). Nonetheless, in 1998 there were only six recruits in the exclosure plot and two and four in its controls. In 1998 the soils inside the fence were still bare, with very little leaf litter and a rough soil microtopography characteristic of pig-rooted areas. The density of seedlings within the

exclosure in 1996 was profound, yet only six grew to 30 cm height after 24 months. Thus, differences reported here in recruitment to the  $\geq 30$  cm size class and seedling number  $< 30$  cm tall might underestimate considerably the actual influences of pigs on small plants.

### **Effects on free-standing lianas**

We expected that changes in the composition of plant life forms would occur as a result of pig activity. If pigs knock over and kill small plants when rooting, the probability of an individual surviving digging should increase with size; taller plants should have more extensive root systems and hence have more anchor support (Bratton 1975). Likewise, potentially fast growing plants, such as lianas, might survive rooting activity better, consequently altering the liana to tree proportions. We found no evidence to support this hypothesis, however, as there were no treatment differences in the percentage of total stems made up of lianas for plants 30 - 100 cm tall or in the recruiting class. It is interesting to note that lianas did compose a high percentage of total, free-standing woody stems  $< 200$  cm tall (25.6%) and of stems between 30 and 50 cm tall (31.9 %) at PFR. These percentages are higher than those reported for lowland Neotropical sites and comparable with other lowland dipterocarp sites (Putz 1983; Putz 1984; Putz & Chai 1987).

This study documented that native pigs play an important role in plant dynamics at the understory level in this Malaysian rain forest. Pigs affected stem density, species richness, growth, and possibly mortality. One caveat of our study is that the current density of pigs at PFR is almost certainly higher than historical levels. Pig populations are probably larger at PFR as a result of the absence of feline predators and the presence of a year-round food supply in the extensive African oil palm plantations surrounding the reserve. On the other hand, an entire suite of large-bodied herbivorous mammals is completely absent from the study area. Although we are unaware of any studies documenting the impacts of large mammals such as deer, elephants, rhinos, wild cattle, and tapirs on tropical vegetation in Southeast Asia, such impacts may be considerable. How the impacts of pigs at their current density at PFR compare with impacts of a complete suite of terrestrial herbivores is difficult to determine. Nonetheless, our results are relevant for other small forest reserves and fragments in Southeast Asia, where local extinction of predators and large herbivores has occurred.

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## CONCLUSION

Results of my studies show that rooting and nest building by pigs are having a strong impact on the understory plant community at Pasoh Forest Reserve. Number of new recruits, diversity, and growth were higher in plots from which pigs were excluded by fences. An estimated 6.0 nests were constructed/ha/year, composed of 117 uprooted saplings and 145 snapped stems. On average, the construction of each pig nest damaged more than 50% of understory saplings from a 244-m<sup>2</sup> area. Nest construction caused an estimated 0.53% annual mortality of trees 1 – 2 cm DBH in the forest, or 28.9% of all mortality for trees of this size class. Furthermore, damage to plants as well as plant response to damage was not uniform across taxa. Dipterocarpaceae, the most dominant plant family at Pasoh, accounting for 25% of aboveground plant biomass, was disproportionately affected. Stems from this economically and ecologically paramount plant family were used in nest construction by pigs twice as often as expected, and more often than any other family. Furthermore, individuals from this family responded poorly to stem damage. Dipterocarps, along with individuals from the Euphorbiaceae, the most speciose tree family, were the two worst plant families in terms of surviving stem damage via resprouting. Conversely, the most successful resprouting species were often understory trees and treelets. Taken together, these results suggest that the future composition of Pasoh Forest Reserve may shift away from the currently diverse and dominant Euphorbiaceae and Dipterocarpaceae towards a subset of prolifically sprouting smaller stature species.

The damage to the understory plant community described here is almost certainly more intense than under more natural conditions due to the extraordinary number of pigs currently inhabiting the reserve. Pig density at Pasoh is among the highest ever recorded from any native habitat and 10 – 100 times higher than historical levels for dipterocarp forests due to the combination of locally extirpated natural predators and an abundant, year-round food supply from the palm oil tree plantations that virtually surround the forest reserve.

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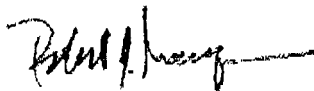
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## VITA

Kalan was born in Washington, Pennsylvania on January 3<sup>rd</sup>, 1970. He finished his Biology degree at Swarthmore College in 1992, and then took a year off from academics. During this time he spent six months working as a research assistant in Borneo and Papua New Guinea while trying to decide what area of tropical ecology to pursue for his graduate work. He chose plants, and enrolled at Louisiana State University under G. Bruce Williamson in 1993. He conducted his dissertation research in Peninsular Malaysia on the effects of wild pigs on plants. He completed a post-doctoral position at Aberdeen University in Scotland with David Burslem. Their research was in Sabah, Borneo, on the importance of biotic interactions in determining tree species distributions in lowland rain forest.