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Population Status and Ecological Preferences of the Palm *Sommieria leucophylla* Beccari in Salawati Island

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Population status and ecological preferences of the New Guinean endemic palm *Sommieria leucophylla* in a lowland forest of the North Salawati Island Nature Reserve were documented at six different habitat types: river bank, hill slope, hill top, intact, disturbed, and converted forests. Population sizes varied spatially and were dominated by seedlings and juveniles, indicating a growing population. Individuals with stem heights of 0-100 cm and stem diameters of 2-3 cm dominated. The stem height class distribution showed a preponderance of individuals in the juvenile stage class and a strong right hand skew typical of populations in which recruitment and mortality were continuous and density dependent, rather than episodic. *S. leucopylla* preferred specific habitats with river bank and intact forest being the most suitable habitat. Although the palm tolerated hill slopes, the populations were low and even suppressed at hill tops, and seemed to be sensitive to disturbance and changes in water table. Mortality was higher among the early stages but very low in adults. There was little recruitment in disturbed sites and no establishment in converted forests. To conserve the most important remaining populations, it is crucial to protect the most suitable sites in the reserve.

Key words: *Sommieria leucophylla*, population status, habitat types, survivorship

INTRODUCTION

Population status, spatial occurrence, and habitat preference of threatened species in the tropics, even in protected areas, is a challenging task for several reasons. First, the patterns of distribution and abundance of species have not been well documented (Batianoff & Burgess 1993; Bawa & Seidler 1998; Scariot 1999; Shapcott 1999; Keith 2000; Vormisto 2002; Vormisto *et al.* 2004; Bachman *et al*. 2004; Salm *et al*. 2007), thus the habitats and geographical ranges of species are poorly known (Kahn & Mejia 1990; Keith 2000; Vormisto 2002; Bachman *et al*. 2004). Second, a large proportion of tropical species are rare, occurring at very low population densities (Moore 1979; Shapcott 1999; Pausas & Austin 2001; Svenning 2001; Vormisto 2002; Vormisto *et al*. 2004). Third, since the last three decades tropical rare plant research has focused on providing information on the synecological relationships and distribution of endangered populations, while threatened species management requires quantitative autecological data produced from field monitoring programmes (Dowe *et al*. 1997; Keith 2000; Higgins & Ruokolainen 2004). Parameters such as the size and number of populations and area of occupancy form the basis for measurable criteria for further conservation actions (Tear *et al*. 1995; Menges & Gordon 1996; Davie & Sumardja 1997; Phillips 1998; Homeier *et al*. 2002; Bachman *et al*. 2004; Cropper Jr & Anderson 2004).

Palms are recognised as increasingly threatened (Johnson 1996; Ferrero 1997) with a total of 222 species identified by the Palm Specialist Group of the Species Survival Commission as highly threatened with extinction (Johnson 1996). Orchids, timber species, and palms are the top three contributors to the Indonesian list of threatened plants, comprising 93, 55, and 31 species, respectively (WCMC 1997). Despite the country diverse palm species (570 species of c.2600 world palm species) and the economic significance to the people as becoming the second most important group after rice (Uhl & Dransfield 1987), Indonesia has the second most threatened species (Critically Endangered, Endangered, and Vulnerable) after Malaysia with a total of 384 species (IUCN 2000), and perhaps as many as 513 species if the Indonesian list of threatened species recorded by the WCMC (1997) is included.

Primary causes of palm habitat loss in Papua are plantation development, extraction activities mainly mining and logging, and human settlements (Ferrero 1997; Bawa & Seidler 1998; Baker 2002; Pemkab Raja Ampat & CI 2006; Marshall & Beehler 2007). Papua has lost much of the lowland forest between 1980 and 2005 with an annual rate of deforestation of c.0.91% (Achard *et al*. 2002; WRI 2002; Marshall & Beehler 2007). The annual deforestation rates of lowland forests in this island have increased dramatically since 1997 in part due to political and economical instability. In the north Salawati Island, illegal logging and mining are the major problems (Marshall & Beehler 2007).

The North Salawati Island Nature Reserve contains one of the most important remaining populations of *S. leucophylla* in the region in which natural regeneration occurs, supporting a complete range of age and size classes. The North Salawati Island Nature Reserve and the adjacent forest is a very important conservation area in West Papua and has vital functions in the regulation of local and regional hydrology, maintenance of biodiversity (Marshall & Beehler 2007), providing a source of renewable bioresources and habitat for various protected plant and animal species (including the endangered birds *Aepypodius bruijnii*, *Paradisaea rubra*, and *Cicinnurus respublica*).

Very little is known about the ecology, habitat requirements, regeneration, and population demography of most New Guinean palm species (Uhl & Dransfield 1987; Dowe *et al*. 1997; Dowe & Ferrero 2000; Maunder *et al*. 2001; Vormisto 2002; Baker 2002), especially those occurred in the lowland rain forests. Consequently, we do not know how to address specific conservation problems and how to set conservation strategies and priorities.

This research aimed to assess and elucidate the population structure, status and demography (stage class, recruitment, and survivorship) of *S. leucophylla* and to elucidate the specific ecological preferences including its habitat specificity. Such information is required to support the reserve management system, particularly through long-term monitoring of at least several, significant populations of *S. leucophylla* occurring on different habitat types. Long-term monitoring programs will provide foundations for developing management system (prescriptions) and conservation priorities for the valuable species and its habitat.

MATERIALS AND METHODS

Study Sites. The North Island Salawati Nature Reserve was established in 1982 based on the decree of the Indonesian Minister of Agriculture No.14/Kpts/Um/II/ 1982, covering a total area of 62,961.96 ha, located in between $130^0$09’00" E and $131^0$03’00" E and between $00^0$54’00" S and $01^0$10’00" S, and lying between Batanta Island and the mainland Papua (Sorong Regency). However, some area of the Reserve (4,550.70 hektar) was converted into settlement and agricultural land in 1996 based on the decree of the Indonesian Minister of Forestry No. 1829/Menhut IV/1996. The current reserve comprises 58,411.26 ha of land area (Pemkab Raja Ampat & CI 2006).

It has the ‘Af’ climate type: tropical wet, experiencing eight consecutive wet months, all months with an average temperature above 18 ^{o}C and small seasonal temperature variations of less than 3 ^{o}C (the Koppen’s System in Tarbuck & Lutgens 2004). The average annual rainfall recorded at a station on Saunek (Waigeo) was 1.5 m.y^{-1}, the daily temperatures ranged from 23 to 33 ^{o}C, with an average humidity of 86%. The wettest months were from April to September. The reserve mainly consisted of hill forests and the land topography was mostly hilly and undulating with slopes ranging from 30 to 80%.

Most area of the reserve was dominated by the New Guinean lowland rain forests, particularly lowland and hill forests on volcanic soils. These two forest types were well represented at Wayar River and the adjacent areas as well as in the south of Solol village. However, a large proportion of lowland forest on sand-stone and alluvium formations occurred outside the reserve spreading from Kapatlap-Samate to the south-west of the island. Scattered mangrove formations occurred in the east and south of the island.

The characteristics of lowland forests in Salawati are generally Malesian, but without the dominance by the family Dipterocarpaceae members as seen farther west. The vegetation structure at the study site (Wayar River) was dominated by lowland species. The main forest canopy (>25 m) consisted of *Intsia bijuga*, *I. Palembanica*, *Artocarpus altilis*, *Pometia pinnata*, *Vatica papuana*, *Koordersiodendron pinnatum*, *Celtis philippensis*, *Semecarpus macrocarpa*, and *Hopea novoguineensis*. The second stratum (upper subcanopy: 15-25 m) was composed by *Dillenia papuana*, *Nageia wallichiana*, *Gyrinops verstaghii*, *Nephelium cuspidatum*, *Leea indica*, *Myristica lancifolia*, *Kjelbergiodendron celebicum*, and *Canarium* sp. The third layer (lower subcanopy: 5-15 m) consisted of smaller trees and shrubs, including *Maniltoa rosea*, *M. plurijuga*, *Tabernaemontana aurantiaca*, *Chisocheton ceramicus*, *Aglaia lawii*, *Popowia schefferiana*, and *Garcinia dulcis*, the palm *Sommieria leucophylla*, *Caryota rumphiana*, and *Cycas ruminiata*. The forest floor (understorey: < 5 m) was mainly occupied by *Licuala graminifolia*, *Pandanus* sp., the ferns *Selaginella wildenowii*, *Elatostema polioneurum*, and *S. leucophylla*. Climbing species included *Piper* sp., *Scindapsus* sp., and the rattan *Korthalsia* sp.

Study Species. *Sommieria leucophylla* Beccari (Arecaceae) is a monoecious, small, solitary, short-stemmed up to 3 m tall with 2-3 cm in diameter, unarmed, pleonanthic palm. The stem is eventually becoming erect, bare, ringed with very close leaf scars, and sometimes bearing aerial roots. The palm is easily recognized by its numerous (20-30), entire (undivided), deeply bifid, leathery leaves, with a distinctive silvery white to golden underside and dark green above. Leaf lengths range from 1.8 m to 2 m consisting of petiole (c.0.4 m in length) and rachis (c.1.5 m in length). Long pedunculate inflorescences arise among the leaves (interfoliar) with peduncle length alone reaching 1.15 m. A single tubular peduncular bract is borne at the tip of the peduncle, enclosing the flowers before anthesis. The short rachis usually consists of 5-6 rachillae (of c.25 cm long each), spirally arranged, bearing a total of 30-40 individual fruits. Fruits are distinctively bright red, small, round or cork-shaped, of 2.5 x 2.0 cm in size. The seed is spherical with homogeneous endosperm and a subbasal embryo. The name *Sommieria* was given to honor Stephen Sommier, a European botanist as a friend of Odoardo Beccari (Baker 2002; Heatubun 2002).

The species is confined to northwestern New Guinea, occupying the undergrowth of the humid lowland rain forest becoming a characteristic component of the forest. The other two used to known species: *S. affinis* Beccari and *S. elegans* Beccari are also confined to New Guinea. All three species are found in West Papua (Irian Jaya). Heatubun (2002) joined the three into a single species: *Sommieria leucophylla* Beccari and consequently regarded the genus as monotypic. *Sommieria* is closely related to *Heterospathe*, particularly to the short-stemmed, undergrowth taxa with sparsely branched inflorescences (Uhl & Dransfield 1987) and to *Pelagodoxa*, with which shares the same curious, warty, albeit much smaller fruits. The taxonomic accounts of *S. leucophylla* were based on Beccari (1877), Uhl and Dransfield (1987), and Heatubun (2002).

S. leucophylla remains unknown ecologically and biologically, and well collected materials are required. Of the 32 indigenous to New Guinea palm genera, only two are endemic: *Sommieria* and *Brassiophoenix* (Heatubun 2002). There has been no comprehensive population and conservation status studies of the distinctive species conducted up today. This species has rarely been used for ornamental purposes. It can be a flagship species to promote conservation of the New Guinean lowland rain forest and has been protected by the Indonesian Government's Regulation 7 1999 on the Preservation of Plant and Animal Species.

Site Selection. Six sites were chosen to study inside the North Salawati Island Nature Reserve to cover a wide range of population structures and sizes, vegetation associations, forest and habitat types, altitudes and aspects, covering river bank, hill slope, hil top, intact forest, disturbed forest, and converted forest. The disturbed and converted forests observed were situated at behind the Solol village. To narrow down the study area, a preliminary survey exploring the reserve was conducted to get access to various sites and cover different habitat types (including potential areas where *S. leucophylla* might be present) before selecting the sites. No herbarium records, plant collections, or existing locality records were available for *S. leucophylla* originating from the reserve before this study.

Population Structure and Status. To assess the population structure and status of *S. leucophylla*, a systematic parallel line sampling was used to ensure that representative samples (parts) of the study area were covered and the target species recorded (Ludwig & Reynolds 1988). Each selected site was sampled into 10 belt transects (of 100 x 10 m each) with the major axis orientated north-south derived from a selected compass bearing. Thus a series of 60 belt transects covering a total area of 6 ha were established at six different habitat types (1 ha for each habitat type). The accuracy of the method was improved by developing belt transects closer together with an interval of 10 m. Each belt transect was located by a Garmin Global Positioning System MAP 175. To develop a full population structure and status, all individuals (comprising seedlings, juveniles and adults) within each transect were measured and counted. To avoid any problems of double counting, all recorded individuals were tagged. Belt transects were set up and investigated in May 2008.

Measurement Attributes. Measurements included the numbers of individual, stem diameter of all individuals with visible stem, height of the visible stem to the base of the leafsheath of the lowest leaf (for juveniles and adults), and leaf size of seedlings (length average of the two oldest live leaves (following Ratsirarson *et al*. 1996). Stem height was measured by a measuring stick and stem diameter by a diameter tape.

Stage Structure. Seven different stage classes were defined within the populations depending on the size (length) of the leaves for seedlings (stem invisible) and the height of the stem for juveniles and adults (stem visible), following Ratsirarson *et al*. (1996). Seedlings were divided into 2 stages due to the wide range of their leaf sizes and each was assumed to have different growth and mortality rates. Juveniles also had a wide range of stem height (consisting of different ages) and were assumed to have different growth and leaf production rates, while adults had different reproductive outputs (i.e. fruit numbers produced by young and old adults as well as the difference in leaf production rates). The categories defined were sedling S_1 (stem invisible, leaf length $\leq$ 100 cm); seedling S_2 (stem invisible, leaf length > 100 cm); juvenile J_1 (stem visible, leaf scars conspicuous, crown shafts developed, and the stem height $\leq$ 50 cm); juvenile J_2 (immature individual with stem height > 50-100 cm); adult A_1 (young adult or mature individual with stem height > 100-200 cm (based on the flowering/fruiting evidence of wild individuals); adult A_2 (mature individual with stem height > 200-300 cm; and adult A_3 (old mature individual with stem height > 300 cm), following Ratsirarson *et al.* (1996).

Habitat Preference (Specificity). To determine species specific habitat preferences, a total of 30 continuous belt transects (of 100 x 10 m each) were established spreading from the bank of the Wayar River (S 00^{0}55'05.0" E 130^{0}52'23.8") to the west to the top of the Wayar hill. Three habitat types were classified along the continuous belt transects, constituting the typical physiognomies of the North Salawati forest and were differentiated on the basis of the distance to water and land incline (drainage quality): *river banks* (wet, flat area to minor slope of 0-30 per cent, comprising near or along river banks), *hill slopes* (humid to dry, slopes ranging from 40 to 70 per cent, well-drained habitat), and *hill top* (dry, moderate slope, relatively open area). Land slopes were measured using a clinometer (SUUNTO). The sites chosen included both natural (intact) and disturbed forests. Based on the forest integrity or disturbance level, three habitat types were described: *intact forest*, *disturbed forest*, and *converted forest* in order to assess the palm abundance in different habitat qualities.

RESULTS

Population Structure and Status. Population structure of *S. leucophylla* was represented in two ways: by stem height class (Figure 1) and stage class (Figure 2). The stem height class distribution showed a preponderance of individuals in the 0.0-0.50 cm height class (29.8%) and a strong right hand skew typical of populations in which recruitment and mortality were continuous and density dependent, rather than episodic. The relative frequencies of individuals in the next two classes (51-100 cm and 101-150 cm) were also important (Figure 1), reflecting a reduced rate of stem growth once stems found a more suitable, exposed layer in the canopy. *S. leucopylla* preferred low to moderate sunlight exposure, occupying mainly the lower subcanopy or understorey (2-4 m). At 1-1.5 m in height plants started to produce flowers, thus more energy might be allocated for reproduction than for vertical growth afterwards.

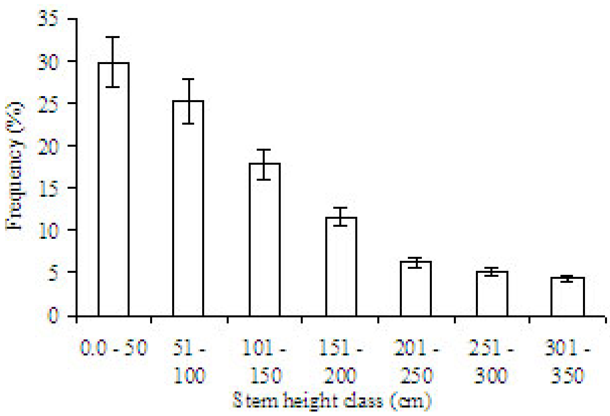

Figure 1. Stem height-class frequency distribution of *S. leucophylla* at the North Salawati Island Nature Reserve, the Raja Ampat Islands, Papua. Tails on each bar are the standard deviation (n = 258).

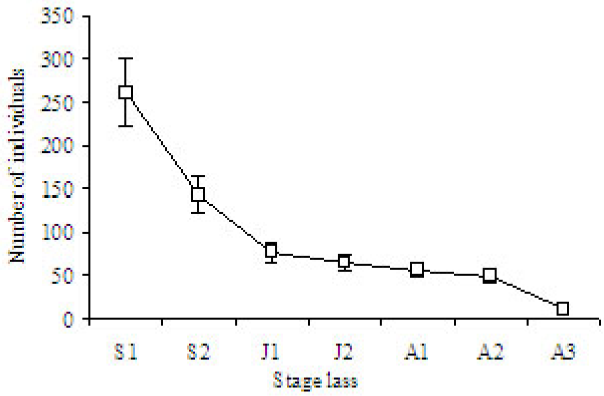

Figure 2. Population structure of *S. leucophylla* by stage class at the North Salawati Island Nature Reserve. Tails on each bar are the standard deviation (n = 662, including seedlings). S_1 (seedling, leaf length ≤100 cm); S_2 (seedling, leaf length >100 cm); J_1 (juvenile, stem visible, stem height ≤50 cm); J_2 (juvenile, stem height >50-100 cm); A_1 (young adult, stem height >100-200 cm); A_2 (adult/mature individual, stem height >200-300 cm; and A_3 (old adult individual, stem height >300 cm).

Figure 2 showed the numbers of individuals surviving in different stage classes. Younger plants tended to dominate at the reserve as indicated by their mean frequency distributions for juveniles, i.e. individuals with stem height 0-100 cm (Figure 1) and number of individuals for seedlings (Figure 2). The number of individuals with stem height > 300 cm (A3, old adults) decreased significantly compared to the previous stage (A2, stem height 200-300 cm), indicating a higher mortality rate during this stage. In general mortality was higher among the early stages of *S. leucophylla* life cycle (particularly during the seedling stage) and was very low in mature individuals (Figure 2).

Relationship between Stem Height and Stem Diameter. The regression line between stem height and stem diameter of *S. leucophylla* indicated that stem diameter increased slowly with the palm height. However, at the height of 150-200 cm the palm seemed to grow slower (Figure 3). The crown position of *S. leucophylla* was in the lower subcanopy and heavily shadowed by taller trees. It is a common phenomenon that subdominant plants or those overshadowed by larger trees are generally slower growing than exposed or dominant species. Such plants will react in various ways, such as reduced height growth and stem size, altered crown architecture and size, development of asymmetric crowns, and even in extreme cases of suppression (Daalen 1993). In order to survive and compete with other plant species, *S. leucophylla* seemed to adapt the environmental conditions by reducing the height growth and stem size.

Habitat Preference (Specificity). Figure 4 showed that *S. leucophylla* preferred specific habitat types, with river bank and intact forest being the most suitable habitat. In contrast, the palm was very rare and suppressed at hill tops. Although the palm still tolerated hill slopes, the populations were generally low. The palm seemed to be sensitive to changes in water table; the mean density on

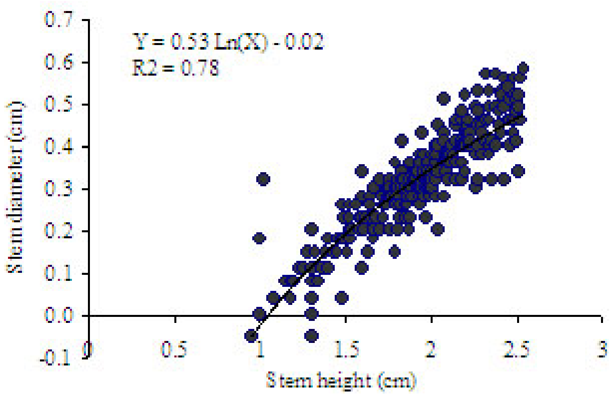

Figure 3. Logarithmic relationship between stem height and stem diameter of *S. leucophylla* at the North Salawati Island Nature Reserve, the Raja Ampat Islands. Stem height and diameter values are Log_{10} (n = 258).

Table 1. Abundance of *S. leucophylla* at different habitat types and disturbance levels (forest integrity) at the North Salawati Island Nature Reserve, the Raja Ampat Islands. The total area sampled was 6 ha (i.e. 1 ha per habitat type)

Habitat type and forest integrity	Number of individuals (ha^{-1})	Slope (%)	Altitude (m asl)
River bank	92	Flat area or minor slope (0-30), wet	154
Hill slope	44	Steep slope (40-70), humid	169-200
Hill top	8	Moderate slope (20-40), open area, dry	210
Intact forest	79	Flat to steep slope (10-70)	154-179
Disturbed forest	33	Flat to moderate slope (10-40)	64-98
Converted forest	2	Flat to moderate slope (10-40)	25-60

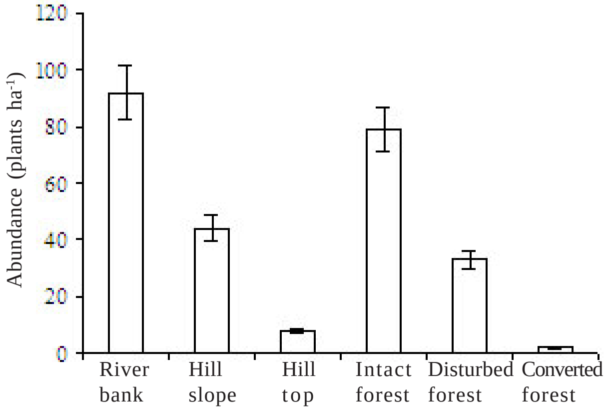

Figure 4. Abundance of *S. leucophylla* at different habitat types (drainage qualities) and disturbance levels within the North Salawati Island Nature Reserve, the Raja Ampat Islands. Tails on each bar are the standard deviation (n = 258).

wet and flat area was 92 individuals ha^{-1}, while that on hill top was only 8 plants ha^{-1}. *S. leucophylla* also seemed to be very sensitive to disturbance; while the abundance on intact forest was 79 stems ha^{-1} that on converted forest was only 2 individuals ha^{-1}. Although the fish tail palm still tolerated disturbances, the populations dropped significantly once the disruption occurred (Table 1). At the forest areas where were totally converted (e.g. into cacao plantation) the palm was not found. Due to the specificity, *S. leucophylla* appeared to have a narrow range of ecological tolerance (amplitude) and formed a good indicator of the New Guinean lowland wet ecosystem.

DISCUSSION

The presence of substantial, recruiting populations of *S. leucophylla* in the Wayar River indicated that the local conditions are favourable for its establishment. Seedlings and juveniles were the most common stages. Assuming the population was in a dynamic equilibrium and age was related to leaf size (for seedlings) or stem height (for juveniles and adults) as observed, population structure will be related to survivorship.

Population structures and sizes varied spatially with river bank areas being the most favourable habitat in which the largest populations occurred. By protecting this habitat type, the populations of this species will be sustained for the long term. This information can be used to set criteria and priorities for protecting representative suitable sites both within and outside the reserve. As seedlings in some locations experienced high mortality, *in situ* management should focus on monitoring the survival of the early stages in order to establish successfully. The slow development of seedlings is the critical step in coping with frequent floodings. Given expected patterns of forest conversion and disturbance over the next few decades, the most important step is to protect high quality habitats (especially river banks and intact forests) in dedicated conservation reserves.

Mortality was higher among the early stages of the life cycle (seedlings) but was low in mature individuals, apart from the current local harvesting rate of adults that was approximately 30 stems $year^{-1}$ (per unit area) in the Wayar River population. This population had an occupancy area of c.300 ha, thus there would be approximately 14,400 adult individuals (300 x 48) in this location, where 48 was the average adult abundance. The number of new individuals established in this population through seed per year ($N*R_0$) was approximately 4234, estimated from: 20% germination x 35 (the mean number of fruits per wild adult individual) x 14,400 (the number of adults) x 4.2% (the percentage of individuals with flowers or fruits during the observation).

The initial high mortality seemed to occur between seedling leaf length classes 1 ($\leq$100 cm, S_1) and 2 (>100 cm, S_2); only 55 per cent of the individuals in S_1 survived S_2. In contrast, a significant decrease in mortality was shown by the juvenile stages (stemmed individuals); 85 per cent of the individuals in J_1 (stem height $\leq$ 50 cm) survived in J_2 (stem height >50-100 cm). Once seedlings grew into stemmed individuals, their mortality rates decreased substantially. A similar decrease in mortality was shown by adult individuals; 88 per cent of the individuals in A_1 (stem heigh > 100-200 cm) survived in A_2 (stem height > 200-300 cm). However, only 21 per cent of seedling individuals reached maturity (A1, young adults) and even only 4.2 per cent of those extended to old adults A3 (Figure 2). A local disturbance was noted as the local communities sometimes used the adult stems as spears for hunting wild pigs. Stems with lengths between 2 and 3 m were preferred because of their hardness and straightness.

Higher mortality among the early stages was likely caused by frequent floodings, severe competition for space, and dense canopy preventing sunlight exposure. The establishment of abundant seedlings may be the palm survival strategy to maintain a successful population recruitment, i.e. survival probability would be expected higher by producing many seedlings. The leaves of young plants are also susceptible to insect attacks while the apical meristem may be eaten by wallaby (*Dorcopsis veterum*).

Local extinction of the populations was quite likely outside the reserve due to continuing land conversion (i.e. for cacao plantation and other agricultural practices). Small vulnerable populations existed in some sites showing an imbalance in stage distribution and very little recruitment (e.g. disturbed forests behind the Solol village). Yet only two young individuals remained at the converted forests where no adults were found from which recruitment may occur. The inclusion of the disturbed and converted sites was intended to promote future monitoring and the need for an integrated landuse management.

Interestingly, seedlings were often not found beneath the crowns of fertile mature plants. Long pedunculate inflorescences (with peduncle length alone reaching 1.2 m) may be the palm survival strategy in order to distribute the seeds away from the mother plants. The absence of the seedlings may be due to physical constraints caused by dense juveniles at the mother plant bases preventing germination. The existence of an allelopathic mechanism seems unlikely. The regeneration strategy of developing many seeds appears to be more effective in areas where floodings occur frequently (Fong 1977).

The first reproduction in *S. leucophylla* was predicted to occur in 15-25 years after germination and seemed to be earlier than that in *Cyrtostachys renda* (25-30 years; Widyatmoko *et al*. 2005; Widyatmoko & Burman 2006), *Neodypsis decaryi* (30-35 years; Ratsirarson *et al*. 1996), and *Astrocaryum mexicanum* (32-36 years; Pinero *et al*. 1984), but was similar to that observed in *Geonoma congesta* (15-29 years; Chazdon 1992). However, in cultivation (e.g. Bogor Botanic Gardens), *S. leucophylla* appeared to grow faster than in the wild. The estimate of longevity in *S. leucophylla* might be shorter than that in *C. renda* (80 years; Widyatmoko *et al*. 2005) and *Welfia georgii* (80 years; Lieberman *et al*. 1988) with an approximate of 40-60 years to reach the maximum height and much shorter than that in *Neodypsis decaryi* (200 years; Ratsirarson *et al*. 1996) and *Astrocaryum mexicanum* (150 years; Pinero 1988).

For plants, stage-structure is more useful for interpreting demographic data than age-structure, because reliable information on the age of immature individuals (i.e. establishment phase) is very limited. In this study, the predicted time taken for *S. leucophylla* individuals to produce stems was 5-10 years based on the plantation data at Bogor Botanic Gardens. The actual time required by wild individuals to reach juvenile stage may be longer than that of the cultivated individuals. In addition, the indeterminate growth or growth plasticity of plants often makes the age-structure a poor predictor of future dynamics (Savage & Ashton 1983; Oyama 1990; Ratsirarson *et al*. 1996) and height has been found to be a better predictor of palm fecundity than age (Ratsirarson *et al*. 1996). Following these authors, height was chosen as a state variable for interpreting population growth in this study.

The influence of slope on soil texture and water holding capacity partly determines the levels of available mineral nutrients, and consequently the establishment and spatial distribution of vegetation. Small variations in elevation can even be important in flat areas such as river banks. Soils on slopes tend to be coarser and better drained than those on flat ground where run-off creates accumulations of small soil particles (House 1984; Kessler 2000; Costa *et al*. 2008). Soils on slopes continually lose their materials and minerals to sites below, thus fertilising the river banks. The mean palm density on flat river banks was 92 individuals ha^{-1}, that on well-drained sites (hill slope) was 44 individuals ha^{-1}, while on very well-drained sites (hill top) it was only 8 plants ha^{-1}. The abundant individuals occurred on flat river banks indicated that flooding might be an important natural event for the palm seed dispersal. The roles of birds and other animals in the palm dispersal mechanism are not yet understood at this stage, suggesting further investigation. As *S. leucophylla* seems to be sensitive to changes in water table, the occurrence of dormancy can also be a vital stage in the palm life cycle and survivorship, particularly for individuals or populations occurred on hill tops and steep slopes. Further information on the palm dormancy is required.

Apart from human disturbance, the most important limiting factor for *S. leucophylla* populations seems to be soil drainage; it cannot tolerate soils in which water shortage occurs for long periods. The behaviour pattern of this palm was different from that of *Cyrtostachys renda* (Widyatmoko 2001; Widyatmoko *et al*. 2005; Widyatmoko & Burgman 2006), *Oncosperma horridum* and *O. tigillarum* (House 1984), where these three later species avoided poorly drained clayey substrates and occasional flooding. Several other studies had also shown that habitat specialization was important for understanding palm abundance and distribution patterns (e.g. Kahn & Mejia 1990; Svenning 1999). It seems crucial to protect river banks and intact forest sites in the Salawati Nature Reserve if we are to conserve the main populations of the valuable endemic species.

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