Spatial Distributions of Wind-dispersed Fruits and Trees of *Swintonia schwenkii* (Anacardiaceae) in a Tropical Forest of West Sumatra

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Abstract The spatial distributions of fallen fruits, seedlings, and trees of *Swintonia schwenkii* (T. & B.) T. & B. were studied in plots totaling 1.86 ha in a tropical foothill forest near Padang, West Sumatra. We recorded the positions of all fruits (2240 mature and 6715 immature), and 572 trees in the plots in September and October 1989. *Swintonia schwenkii* was the dominant emergent in the plots, and had eight canopy-to-emergent trees from 36 to 62 m in height. Seven of them produced fruits. There were no *S. schwenkii* of $20 < H \leq 36$ m in height. An index of spatial association showed that *S. schwenkii* in the seedling-to-pole layer ($0 < H \leq 20$ m) tended to be distributed away from those of conspecific emergent trees.

The mature fruits are 2 g in fresh weight, having five wings 6×1 cm in size and one seed inside. In contrast with the distribution of seedlings and small trees, many fruits dropped under the crowns of mother trees. The number of fruits decreased exponentially with distance from a mother tree, and fruits dispersed further than 50 m were rare.

Key Words: wind dispersal / *Swintonia schwenkii* / spatial distribution / population dynamics / tropical forest

The spatial distribution of plants in a community gives us important implications for understanding the dynamics of populations (Augspurger, 1983). It has been studied for many plant species. Most of the studies, however, have treated plants in the stage after establishment. Comparison of the distributions at different stages of the life history will clarify the dynamics more precisely. The dynamics of tropical trees have not been sufficiently studied, even of the common and dominant species. *Swintonia schwenkii* (T. & B.) T. & B. is one of them. It reaches more than 60 m in height, and is one of the dominating emergents in Sumatran tropical foothill forests. In permanent plots in Padang, West Sumatra, *S. schwenkii* made the biggest crop of fruits in 1989 during the several survey periods since 1979. We could find easily the long-winged and green- or red-colored fruits on the brown forest floor.

In tropical forests, some trees make wind-dispersed fruits. Their dispersal distances have been observed only in a few species (Ridley, 1930; Burgess, 1970; Augspurger, 1983). There is no study about the fruit dispersal of *S. schwenkii*. Here we report on fruit dispersal and spatial distribution of trees of *S. schwenkii*, and discuss the adaptive significance of winged fruits.

STUDY SITE AND METHODS

The study area was on a hill side of Gunung (Mount) Gadut in the Barisan Mountains, situated 18 km east from the coast of Padang, West Sumatra. In Padang city the annual precipitation is about 4764 mm/yr and annual mean temperature is 27.0 °C (Hotta ed., 1984). Hotta

Fig. 1. A, positions of immature and mature fruits on the forest floor in PIN Plot. Crown projection and root collar of emergent trees of *S. schwenkii* (36 - 62 m high) are also shown. A tree drawn with broken line did not flower in 1989. B, topography of the PIN Plot (from Hotta ed., 1984). A dot line shows a trail.

and other scientists had established permanent plots, and we used two plots of theirs: the Pinang-Pinang (PIN) Plot and the Gajabuih (GAJA) Plot (Hotta ed., 1984). The PIN Plot was established in 1981 on a ridge top (Fig. 1B) 590 - 620 m in elevation (Lat. 0° 55' S; Long.

Fig. 2. A, positions of seedlings and trees in the PIN Plot. Crowns and root collars of emergent trees are also shown. B, gaps (open) and closed (shaded) stands in 1987. Grids of 10×10 m, and 20×20 m are used for the calculation of ω (Iwao, 1977), of which results are given in Table 2.

$100^{\circ} 30' E$). The GAJA Plot was established in 1980 on a slope (Fig. 4B) 1.5 km south-south-east of PIN Plot at 590 - 635 m in elevation. The GAJA Plot had an area of 0.9054 ha, and we used a part of the plot area of 0.86 ha as shown in Fig. 3. There were no emergent trees of *S.*

Table 1. Number and basal area of trees, and number of fruits of *Swintonia schwenkii* in two plots.

Plot	PIN	GAJA
Area (ha)	1.00	0.86
Total basal area (m ² /ha)	39.9	27.0
<i>Swintonia schwenkii</i>		
Basal area (m ² /ha)	4.9	1.5
Maximum height (m)	57.5	61.7
Maximum DBH (cm)	132.0	102.7
No. of trees (/plot) in each height class		
seedling 0 < H ≤ 1 m	167	41
sapling 1 < H ≤ 10	129	200
pole 10 < H ≤ 20	12	15
(canopy tree) 20 < H ≤ 36	0	0
emergent tree 36 < H ≤ 62	6	2
No. of immature fruits (/plot)	124	6591
No. of mature fruits (/plot)	973	1267

schwenkii in the peripheral zones of about 50 m width surrounding these two plots. We considered that fruits dispersed into the plots from outside were rare.

The trees bigger than 8 cm in diameter at the height of 1.3 m above the ground (DBH) had been measured repeatedly since the establishment of the plots. The DBH values and the heights of some species including *S. schwenkii*, were measured again from 13 August to 3 October 1989. Further, we measured height (H) and position of seedlings and small trees of *S. schwenkii* less than 8 cm in DBH from 11 September to 2 October 1989. We recorded the positions of mature and immature fruits of *S. schwenkii* on the forest floor on 7-8 October in the PIN Plot and 9-12 October in the GAJA Plot. We picked off wings from recorded fruits, and returned wingless fruits to the same position for distinguishing them from non-recorded fruits.

RESULTS

Structure of the forest

Swintonia schwenkii was the most dominant species in both plots. Its basal area (BA, sum of stem cross sections at the height of 1.3 m) occupied 12% and 6% of the total BA of trees in the PIN Plot and the GAJA Plot, respectively (Table 1). Other common canopy or emergent trees were *Lithocarpus* spp., *Castanopsis rhamnifolia*, *Nephelium juglandifolium*, *Dialium* sp., *Shorea maxwelliana*, *Hopea dryobalanoides*, and so on. *Swintonia schwenkii* had no trees in the height class of 20 < H ≤ 36 m and was completely separated into two layers of the forest profile in the two plots. There were eight trees in the height class of 36 < H ≤ 62 m (emergent); 564 individuals were seedlings (0 < H ≤ 1 m) or saplings-to-poles (1 < H ≤ 20 m). We distinguished the latter into saplings (1 < H ≤ 10 m) and poles (10 < H ≤ 20 m).

Distributions of fallen fruits and trees in the PIN Plot

Figure 1A shows the positions of fruits of *S. schwenkii* on the forest floor of the PIN Plot. There were six trees forming the emergent layer of the PIN Plot. They all flowered except

Fig. 3. Positions of immature fruits on the forest floor in the GAJA Plot. The crowns of trees of *S. schwenkii* no. 354 and no. 381 are shown in the upper part and lower part of the plot, respectively. The root collar of standing dead *S. schwenkii* is shown in the right side. In the rectangular area around the tree no. 354, the density of fruits (per 3.31 m²) are presented. The area enclosed with broken line were included in the permanent plot though we did not survey.

one of 55 m in height whose crown is drawn with broken line in Fig. 1A. The individuals in the sapling-to-poles class did not flower. *Swintonia schwenkii* produces panicles with many small flowers. It seemed that only a few of the flowers had developed into mature fruits. We distinguished the fruits into mature and immature. We measured 15 mature fruits: the minimum, average, and maximum fresh weights of them were respectively 1.1, 2.0, and 3.1 g, and mean dry weight was 0.79 g. Five petals surrounding stamens at flowering are reflexed in fruit and become wings. The mean length and width of the longest of the five wings of each fruit were 5.8 and 1.0 cm. The five wings of each fruit were about the same size. The mean length and diameter of the elliptical drupe were 2.4 and 1.1 cm. Each drupe had one exalbuminous seed. The immature fruits were smaller than mature fruits, and especially the drupe had not developed.

During the survey time, trees of *Canarium* sp. (Burseraceae) produced many drupaceous fruits with fleshy pericarp. The fruit size was similar to a drupe of *S. schwenkii*. Many monkeys ate the *Canarium* fruits. We found many eaten fruits of *Canarium* on the forest floor though no eaten fruits of *S. schwenkii*.

There were many mature and immature fruits under and near the crowns of the fruiting

Fig. 4. A, positions of mature fruits on the forest floor in the GAJA Plot. Crowns and root collars of emergent trees are also shown. Three domains marked A, B and C are defined for analysis of dispersal distance (cf. Fig. 5). B, topography of the plot. (from Hotta *et al.*, 1984)

trees. The number of fruits decreased with increasing distance from the emergent trees. The distances of immature fruits of *S. schwenkii* seemed to be about the same with the mature ones. This result disagrees with the observation of Ridley (1930) that lighter immature fruits of *Shorea* could reach more distant places. Some of the mature fruits had germinated when we studied them. Thus these fruits seemed to have no dormancy.

The positions of trees and seedlings of *S. schwenkii* in the PIN Plot are shown in Fig. 2A. The 12 trees in the pole class ($10 < H \leq 20$ m) did not grow under the crowns of *S. schwenkii* of the emergent layer. A few of the seedlings ($0 < H \leq 1$ m) and saplings ($1 < H \leq 10$ m) were found under the crowns. Fig. 2B shows the tree fall gaps in 1987 (Kohyama *et al.*, 1989). The distribution of the seedlings, saplings-to-poles and the fruits seemed to have no relationship with the positions of the gaps.

Distributions of fallen fruits and trees in the GAJA Plot

The positions of immature and mature fruits in the GAJA Plot are shown in Fig. 3 and Fig. 4, respectively. The GAJA Plot had two emergent *S. schwenkii*: tree no. 354 of 45 m high, and tree no. 381 of 61.7 m high. Both trees flowered and their crown areas were 105 and 234 m² respectively. There were 6591 immature fruits on the GAJA Plot while only 124 on the PIN

Fig. 5. The relationship between distance from the tree no. 381 and density of mature fruits in three domains, A, B and C as shown in Fig. 4.

Plot. Immature fruits were concentrated around the tree no. 354. In a rectangular area of 12.2×17.1 m around the tree, we found 5978 immature fruits. On the contrary, there were few immature fruits around tree no. 381. The tree no. 381 flowered earlier than no. 354 and the most of its immature fruits had already decayed, which was also the case in the PIN Plot.

The dispersal distances of mature and immature fruits were not different from each other in the PIN plot. Thus we can suppose that most of the mature fruits in three domains A, B, and C shown in Fig. 4, where there were few immature fruits from tree no. 354, came from tree no. 381. Figure 5 shows the relationships between the distance from the root collar of no. 381 and the density of mature fruits on the ground. The densities of fruits seemed to decrease exponentially with increase in distance.

Figure 6A shows the position of trees in the GAJA Plot. There were no individuals of the seedlings, saplings and poles under the emergent crowns of *S. schwenkii*. A big standing dead *S. schwenkii* might had produced some sapling-to-poles before it died between 1984 and 1987. We found no seedlings and saplings under the crowns of living *S. schwenkii* or under the crown of the dead tree. Forty-two percent of the area of the GAJA Plot was tree-fall gaps in 1987 (Table 3). Many seedlings and saplings were in the gaps but they also occurred in closed stands.

The topographies of the two plots are shown in Fig. 1B and Fig. 4B. The distributional patterns of fallen fruits and trees seemed to have no clear relationships with the topography.

Table 2. The values of spatial association index ω (Iwao, 1977) between different developmental stages of *S. schwenkii*.

H (m)	The PIN Plot			The GAJA Plot		
	seedling	sapling/ pole	emergent	seedling	sapling/ pole	emergent
	0 - 1	1 - 20	20 <	0 - 1	1 - 20	20 <
5×5 m quadrats						
fruit	-0.07	0.11	0.13	-0.32	-0.73	0.32
seedling		0.25	-0.13		0.02	-1.00
sapling/pole			0.00			-1.00
10×10 m quadrats						
fruit	-0.02	0.18	0.26	-0.35	-0.70	0.72
seedling		0.35	-0.46		0.00	-1.00
sapling/pole			-0.47			-0.80
20×20 m quadrats						
fruit	0.02	0.42	0.53	-0.16	-0.63	0.79
seedling		0.31	0.08		0.03	-0.40
sapling/pole			0.17			-0.76

Table 3. Area and number of fruits and trees of *S. schwenkii* in two sites: under the crowns of emergent *S. schwenkii* and in the gaps. *B* index in the text is also shown. Asterisks show significance of *B* value by χ^2 test (* $P < 0.05$; ** $P < 0.01$).Seedlings: $0 < H \leq 1$ m. Saplings: $1 < H \leq 10$ m. Pole: $10 < H \leq 20$ m.

	Whole plot	Under crowns <i>B</i>		In the gaps <i>B</i>	
The PIN Plot					
Area (m ²)	10041	1777		1676	
Mature fruits	973	350	2.03**	47	0.29**
Seedlings	167	23	0.78	28	1.00
Saplings	129	17	0.74	27	1.25
Poles	12	0	0	2	1.00
The GAJA Plot					
Area (m ²)	8600	339		3631	
Mature fruits	1267	498	9.97**	163	0.30**
Seedlings	41	0	0	24	1.39*
Saplings	200	0	0**	142	1.68**
Poles	15	0	0	7	1.11

Spatial correlation between different stages

The relations between the distributions of fruits and of trees of different layers were analyzed using the ω index of Iwao (1977). $\Omega = 1$ when the distributions of two species are completely the same, $\omega = 0$ when they are independent and $\omega = -1$ when they are completely exclusive. We divided plots into three types of quadrats, 5×5 m, 10×10 m, and 20×20 m. The latter two types can be seen in Fig. 2B and Fig. 6B, and four 5×5 m quadrats were set in each 10×

Fig. 6. A, position of seedlings and trees in GAJA Plot. Crowns and root collars of emergent trees are also shown. B, gaps (open) and closed (shaded) stands in 1987. Grids of 10×10 m, and 20×20 m are used for the calculation of ω (Iwao, 1977), of which the results are given in Table 2.

10 m quadrat. Because of the polygonal shape of the plots, we could not divide whole plot into the quadrats. We used 80% of the area in the PIN Plot and 84% of the area in the GAJA Plot. The results are given in Table 2.

The values of ω between the emergent trees in $H > 36$ m class and fruits were always positive in both plots and in different quadrat sizes. (There were no trees in $20 < H \leq 36$ m.) It resulted from the dispersal of fruits near the emergent trees. On the contrary, the values of ω between the emergent trees and seedlings ($0 < H \leq 1$ m) were always negative. The areas near the emergent trees seemed to be not suitable for the survival of seedlings though many fruits were dispersed there. The fruits usually germinated soon after dispersal without dormancy, and many had germinated under the canopy. The values of ω between the emergent trees and saplings-to-poles ($1 < H \leq 20$ m) were usually negative but slightly positive in some cases. The ω between fruits and seedlings was usually negative and ω between seedlings and saplings-to-poles was always positive.

The index ω depends on the central points of plants. However, tree crowns cover a given area and may affect plants in the area. The area of tree-fall gaps may also influence plant

distributions. To evaluate the effect of such a site mosaic we introduce the following index of site association:

$$B = \frac{\text{Ratio of plants in a given site to total plants in plot}}{\text{Ratio of the area of a given site to whole plot.}}$$

If the plants are distributed independently to the site, we expect that $B = 1$. If they are more associative to the site than to other places, B is larger than one. We can also carry out χ^2 test for the effect of site mosaic. Table 3 shows the value of B and the result of χ^2 test for sites under the crowns of *S. schwenkii* and for gap site. The crowns covered 17.7% of the PIN Plot area, and 36.0% of mature fruits under the crowns. B of fruits for sites under *S. schwenkii* crowns is 2.03, thus they tended to be associated under the crown. B of fruits for gap sites is 0.28, suggesting that smaller numbers of fruits were dispersed into the gaps. The values of B of seedlings, saplings and small trees under the crowns were less than one in both plots, though the results of χ^2 test were insignificant. The values of them for the gap site were equal to or a little bigger than one.

DISCUSSION

In the tropical zone, a number of dominant species produce wind-dispersed fruits. According to Ridley (1930), most Dipterocarpaceae and *Parishia* of the Anacardiaceae have fruits with wings developed from sepals: *Swintonia*, and *Melanorrhoea* of the Anacardiaceae have fruits with wings developed from petals: *Koompassia* of the Leguminosae has thinly flattened one-seeded dry fruits (samara). They are common and often dominant species in the climax forests of tropical Asia. Thus wind seems to be one of the important agents for dispersal of propagules, though the wind in the tropical zone is not so strong. The above-mentioned fruits were too heavy to be dispersed for a long distance. The dispersal distances of Dipterocarpaceae and *Koompassia* recorded by Ridley (1930) were less than 100 m. Thirty-eight percent of fruits of *S. schwenkii* were dispersed under the crowns of mother trees. The wings were not sufficiently efficient appendages to disperse the fruits far from the mother crowns. The fruits would be, however, more concentrated under the crowns, if they did not have wings.

There were no poles of *S. schwenkii* under the conspecific crowns, though many fruits had dispersed there. The value of ω showed a tendency of exclusive distribution of seedlings and emergent trees of *S. schwenkii*. The micro-environment in the area around mother trees seemed not to be suitable for the survival of younger *S. schwenkii*.

These contrasting distributions of fruits and seedlings around mother trees have been pointed out for many species in tropical forests (cf. Janzen, 1970; Clark & Clark, 1984). Janzen suggested that the exclusion of seedlings around mother trees is one of the mechanisms maintaining the species richness and structural complexity of tropical forests. Hubbell (1980), however, has opposed this hypothesis. Several causes of low survival rate around mother trees have been proposed, such as pathogens (Augspurger, 1983), post-dispersal seed predators (Janzen, 1970), and allelopathy (Webb *et al.*, 1967). We need further studies to get conclusions for these questions.

Fruits dispersal into gaps was not so frequent (Table 3). Gaps are often situated too far from mature *S. schwenkii* tree for fruits to be dispersed there by wind. Augspurger & Franson (1988) reported, however, that wind-dispersed seeds of trees and lianas collected more in

gaps than under closed canopies on Barro Colorado Island, Panama. Some of them may have longer dispersal distances than *S. schwenkii*, and thus arrive at the gaps more easily. *Swintonia schwenkii* seemed not to be a gap-demanding species for their regeneration, because densities of the seedlings, saplings and poles under the canopies of other species were similar to those in gaps. Hence, the fruit dispersal into gaps is not important for this species.

We can thus conclude that the wings of *S. schwenkii* fruits play a significant role by dispersing the fruit under the crowns of other species, and escaping from hazardous place for seedling survival around mother trees.

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鈴木英治, 甲山隆司 西スマトラ州の熱帯林における *Swintonia schwenkii* (ウルシ科) の風散布果実と樹木の空間分布

熱帯林で超出木となる *Swintonia schwenkii* は風散布果実をつくる。この種の地表に落ちた果実と実生を含むすべての個体の位置を調べ、その分布を比較検討した。調査は、インドネシアの西スマトラ州パダン市近郊の熱帯山麓林にある 2 つの調査区 (合計 1.86 ha) 内で、1988 年 8 月から 10 月に行った。*Swintonia* の果実は、湿重が 2 g あり、花弁が変化した長さ約 6 cm、幅 1 cm の羽根を 5 枚持っているため、林床に落下したものを容易に見つけ出すことができた。

実生から最高樹高 61.7 m の超出木までの個体数は 572 本であったが、樹高 20 m から 36 m の間の個体は存在せず、高木から超出木の階層と、20 m 以下の低木層に分れていた。樹高 32 m 以上の個体は 8 本であったが、そのうち 7 本が開花した。20 m 以下の個体は開花しなかった。巖の w の指数によって樹高 32 m 以上の個体と、20 m 以下の個体の空間分布を調べると、両者は排他的に分布していた。有為な差はないが、*Swintonia* 超出木の樹冠の下には *Swintonia* の実生と低木が少ない傾向があった。

果実は、未熟果が 6175 個、成熟果が 2240 個あった。*Swintonia* の実生や低木の分布とは異なり、果実は親木の近くは多く、遠ざかるにつれて指数関数的に減少した。親木の根元から 50 m 以上遠くまで到達した果実は稀であった。

調査区の 29 % が林冠のギャップで、残りは閉鎖林分にであった。*Swintonia* の果実は、風散布であっても遠くまでは飛ばないので、ギャップまで到達した果実は少なかった。実生の個体数は閉鎖林分よりギャップに 1.14 倍多いだけであり、*Swintonia* 実生の発生と生残にとって、ギャップの存在が必須のものではないようだ。したがって、ギャップまで果実が到達する必要性も少ない。だが閉鎖林分であっても、同種の樹冠下よりも別種の樹冠下のほうが、実生の生存には好適のようだから、羽根によって重力散布の場合よりも親木の直下に落ちる可能性を減少させることは、実生の生残にとって意義があると考えられる。ほかにマレーシア熱帯ではウルシ科の *Melanorrhoea* とフタバガキ科が、ガクから変化したものであるが *Swintonia* とよく似た形態と機能を持つ羽根付きの果実をつくる。いずれも高木から超出木になる種群であり、同じような意義があると類推される。