

# Short-distance dispersal of intact Taiwan sassafras fruits in a temperate montane rain forest of northeastern Taiwan

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**ABSTRACT.** The objectives of this study were to understand the within-habitat intact (both mature and immature) fruit dispersal patterns of Taiwan sassafras (*Sassafras randaiense* Rehder), a fleshy-fruited species endemic to Taiwan, and to investigate whether wind could be an important short-distance dispersal agent for the species. Collection traps were placed beneath the crowns of five isolated Taiwan sassafras trees located in a montane rain forest of northeastern Taiwan during the fruiting seasons of 1999 and 2000. Short-distance (up to 8 meters) dispersal patterns in number, size, and fresh weight of dispersed intact fruits were analyzed with distance from parents and dispersal direction as the explanatory variables. Results showed that damaged fruits, which were mainly fruits consumed by rodents, accounted for about 74% of the total fruits collected over the two-year period. Though the numbers of intact fruits collected were about the same in both years, more mature fruits were collected in 1999 due to the absence of a typhoon at the study site that year. The intact fruits collected in 1999 were also larger and heavier. Within a given year and when both years were combined, matured fruits were slightly larger, but were almost twice as heavy as the immature ones. For the intact fruits, analyses revealed that (i) due to gravity most of the fruits were deposited close to the parents, (ii) more fruits were deposited in the north-bearing directions, due to local topography and the prevalent wind directions during the dispersal season, (iii) the dispersal curves in number were similar in most of the directions, (iv) the size of the deposited fruits showed no significant difference with respect to distance and directions, and (v) fruits deposited immediately beneath the crown and some distance away from the focal trees were heavier than those deposited between. The observed spatial dispersal patterns in the number and the weight of intact fruits all suggested that, besides gravity, wind could be an important short-distance agent in dispersing Taiwan sassafras.

**Keywords:** Anisotropic dispersal; Fleshy-fruited; *Sassafras randaiense* (lauraceae); Wind assisted dispersal.

## INTRODUCTION

For plant species, seed dispersal is one of the main factors that decide the quantity and the dynamics of seedlings, as well as the genetic and spatial characteristics of the next generation (Harper, 1977). Describing dispersal patterns and curves, which summarize the relationship between the deposited seed characteristics and the distance from their parents, is the first step toward an understanding of the importance of seed dispersal. Possible dispersal strategies are inferred from these dispersal patterns and

curves (Harper, 1977; Willson and Traveset, 2000; Levin et al., 2003).

In ecology and evolutionary biology, the dispersal of fleshy fruits is of great interest because it provides opportunities to test various adaptation and coevolution hypotheses (Howe and Smallwood, 1982; Stiles, 2000). Avian dispersers, especially birds, are usually considered to be the main agents in shaping the dispersal curves of fleshy-fruited species (Jordano, 2000; Kollmann, 2000; Stiles, 2000). Long-distance dispersal of such species has been the focus of numerous studies for the past two decades. Such a dispersal represents an opportunity for plant species to establish and expand populations in far away places (e.g., Wenny, 2000a). However, a seed dispersal pattern is rarely shaped by a single dispersal agent: most of the dispersal curves have multiple peaks (Levin et al., 2003). For fleshy-fruited species, peaks

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near the parents are often ignored, and their significance in maintaining the local populations is thus overlooked. While fruits or seeds dispersed within-habitat might suffer from keen competition, such a dispersal mode nonetheless might represent a safe or conservative strategy in maintaining the existing population (Wenny, 2000b; Godoy and Jordano, 2001). Thus, short-distance dispersal of fleshy-fruited species, in particular the dispersal of their intact mature fruits, should be examined more closely.

The main goal of this study was to understand the within-habitat intact fruit dispersal patterns of Taiwan sassafras (*Sassafras randaiense* Rehder), a fleshy-fruited species endemic to Taiwan, in a montane temperate rain forest. Though the species is not endangered, its sapling leaves are believed to be the sole food source for the caterpillars of the endangered Taiwan broad-tailed swallowtail butterfly (*Agehana maraho* Shiraki & Sonan). Thus, to protect and restore the population of this endangered butterfly, an understanding of the reproductive biology and natural establishment of Taiwan sassafras is critical.

Besides understanding the short-distance dispersal patterns, we also intended to examine whether wind could also be an important short-distance dispersal agent. Our interest in the question originated from the observations that the fruits of the species are small and light-weighted. And during the dispersal season, strong winds are frequent in the study area because of local topography and summer monsoon winds. Under the density-dependent hypothesis of Janzen-Connell (Janzen, 1970; Connell, 1971) and the escape hypothesis proposed by Howe and Smallwood (1982), we hypothesized that for wind to play an important role in short-distance dispersal, we should observe some intact mature fruits of Taiwan sassafras being deposited away from the immediacy, but still within the neighborhood, of the parents.

## MATERIAL AND METHODS

### Study site

The study site was located at the Chilan-Shan Forest District (24°34' N, 121°23' E) of northeastern Taiwan, which has an elevation of about 2,000 m. The annual mean temperature is 13°C (25°C in the summer and 8°C in the winter), and the annual mean precipitation is about 4,500 mm per year. In Taiwan, the northeastern region is a distinct floristic region with the highest precipitation and cloud frequency on the island (Hsieh et al., 1994). The high precipitation is the result of typhoons in the summer and northeastern monsoons in the winter. The potential main vegetation type of the study site is montane mixed conifer and hardwood rain forests. The slope of the study site was about 20°, tilting toward the northwest. Originally dominated by Taiwan yellow false cypress (*Chamaecyparis obtusa* var. *formosana*), the study site was clear cut in 1977. Immediately after the logging, Taiwan yellow false cypress, Taiwan red false

cypress (*Chamaecyparis formosensis*), and Taiwan cedar (*Taiwanina cryptomerioides*) were planted. Currently, the site is dominated by the planted species, but in areas that remain relatively opened, naturally regenerating Taiwan sassafras is the dominant species.

### Study species

Taiwan sassafras (*Sassafras randaiense* Rehder, Lauraceae) is medium-sized, deciduous tree species that grows in the Taiwan montane temperate rainforests at elevations of 1,100 to 2,500 m asl. Its flowers are polygamous. Its fruits are globose, fleshy, about 6 to 7 mm in diameter, attached to a thickened pedicel, dark-bluish when ripened, and one seed per fruit (Liao, 1997). The seed is believed to have a deep dormancy and long persistence in soil, an atypical syndrome in Lauraceae (Lin, 1992). The species is abundant in open, recently disturbed habitat (e.g., logged or burned forests, road-sides) although seedlings can also be found in the forest understory, where the forest floor is disturbed. Once established, the species can maintain or even expand itself locally. In the study area, which is at the northern distribution limit of Taiwan sassafras, flowering of the species usually starts in late November or early December of the previous year and continues until late January or early February of the next year. Fruits start ripening in late June to early July, and by late August, most of the fruits are either fallen or consumed by animals. In the study area, predation by rodents (mainly Taiwan red-bellied squirrels, *Callosciurus erythraeus*) is the biggest threat to the fruits during the ripening period (89% of the fruits predated, cf. Tsai, 2000). Rodents damage the seed's embryonic tissue, rendering it unviable. Our field observations suggested that birds play an important role in the dispersal, in particular the long-distance dispersal, of the species (Tsai, 2000). Seeds of mature fruits could also germinate without being consumed first. In the field the germination rate of intact fruits is 11-14% (Hu and Ku, 1980; Wang et al., 1986).

### Fruit collection methods

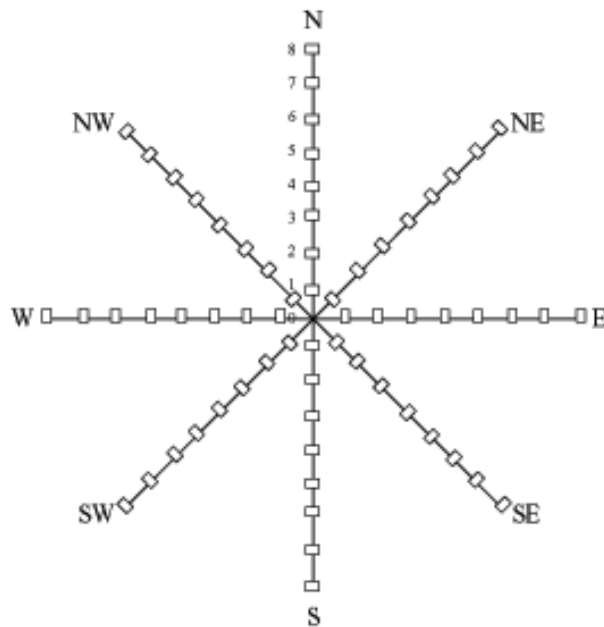
In March of 1999, five isolated, fruit-bearing trees in an open 5-ha area dominated by Taiwan sassafras were selected for this study. The five trees each had plenty of fruits in that year, a fully isolated and healthy tree crown, and good growth vigor. The age of each tree was determined by coring the tree 0.3 m above the ground. The basic information for the five trees is given in Table 1.

For each focal tree, with the stem as the center and starting from north, an 8-meter line transect was laid every 45°. Plastic seed traps (52 cm × 40 cm × 8 cm) were installed every meter along each transect (Figure 1). A total of 320 traps (5 trees × 8 transects per tree × 8 traps per transect) were placed. The transect length was limited to 8 m because a longer transect would produce overlapping seed shadows. Animal repellent was added to the seed traps twice a month to prevent the removal of fruits by animals.

**Table 1.** Basic information on the five Taiwan sassafras (*Sassafras randaiense*) trees observed in this study. The age of each tree was determined by counting the rings obtained from coring the tree at 0.3 m above the ground.

Tree ID	Age	Height (m)	DBH (cm)	Crown Radius (m) <sup>a</sup>	Crown Length (m)
1	21	13.3	26.5	6.5	9.2
2	22	8.5	17.0	4.5	5.3
3	21	10.5	25.0	5.4	8.6
4	18	11.7	22.5	4.3	8.3
5	15	6.9	17.4	3.7	1.6

<sup>a</sup>Averaged based on the crown radii of eight directions.



**Figure 1.** Fruit trap lay-out used in the study.

Dispersed seeds were collected weekly during the summers of 1999 and 2000. In 1999, field work started in early July and lasted until late August, for a total of nine collections. In 2000, work started in late June and lasted until mid-August, for a total of eight collections, after which the study site became inaccessible for three months due to a typhoon. Collected fruits were divided into three categories based on appearance: intact fruits, damaged fruits, and digested fruits. Intact fruits included both mature (outer skin intact and bluish purple in color) and immature (outer skin intact but greenish in color) fruits. Damaged fruits included fruits desiccated and damaged (broken outer skin and damaged seed) mainly as a result of predation by rodents. Digested fruits (without outer skin but seed intact) were mainly comprised of fruits consumed and then excreted or regurgitated by birds. Intact fruits were measured individually for their size (diameter along the long axis, mm) and fresh weight (g). Since digested fruits, which accounted for only a minor portion of the fruits collected (less than 1%), might have been from trees other than the focal trees (or even from trees outside the study area) and were not the focus of this study, they were not included in the subsequent detailed analyses. Although

both intact and damaged fruits collected beneath a canopy might also come from other parents, based on our field observations we considered that unlikely. We thus made the explicit assumption that all the intact and damaged fruits collected within the 8-meter radius of a focal tree were from that tree only.

**Statistical analyses**

Spearman’s rank correlation (Neter et al., 1996) was used to analyze the relationships between individual tree attributes and the number of dispersed fruits (each year and both years combined), and the numbers of fruits individual trees dispersed in the two dispersal seasons. Since damaged fruits were not viable, they were not included in dispersal pattern analyses. For dispersal patterns, we combined the data from the two years and ignored individual tree effects since preliminary analyses showed that year-to-year variation and tree attributes did not contribute significantly to patterns of variation. After converting the dispersed density of intact fruits from a per trap basis to a per m<sup>2</sup> basis, we used a negative binomial regression model to analyze the average dispersal density (number of fruits m<sup>-2</sup>) as a function of direction, distance, and their interactions. As an extension of Poisson regression, negative binomial regression can provide a better fit when the assumption that the mean equals variance under Poisson regression is not met (Allison, 1999). For fruit size and weight, general linear models were used with direction and distance as the independent variables, and mean fruit size and fresh weight at each combination of direction and distance as the response variables. Regular ANOVA assumptions were checked to insure the validity of statistical inferences. The distributions of fruit size and weight did not significantly deviate from normality and equaled variance assumptions. For correlation analyses, we used the SAS statistical software (procedure PROC CORR); for negative binomial regression, we used SAS PROC GENMOD; and for general linear model analyses, we used SAS PROC GLM (SAS, 2000).

**RESULTS**

**Parental effects and temporal patterns**

Among the individual tree attributes measured, tree height showed a significant and positive correlation with

the number of fruits (both intact and damaged) collected in 1999 (Spearman's  $r=1.0$ ,  $p<0.001$ ). Tree age had a significant and positive correlation with the number of damaged fruits collected in 2000 (Spearman's  $r=0.97$ ,  $p<0.02$ ). Measured tree attributes showed no significant effects with either the size or the fresh weight of the collected intact fruits.

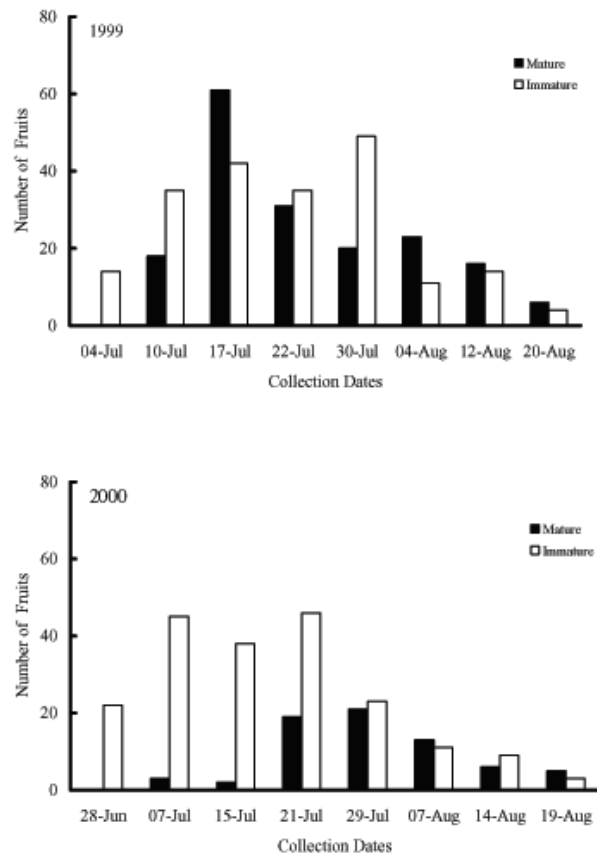
Excluding digested fruits, the total numbers of fruits were roughly the same in 1999 and 2000 (Table 2). For both years, most of the intact fruits were collected in July (Figure 2), and the mean size and fresh weight of the collected intact fruits were about the same throughout the collection periods. In 1999, mature fruits accounted for about 45% of the intact fruits collected while in 2000 the number was about 25%. However, the average size and weight of the intact fruits showed significant differences between the two years, with the intact fruits collected in 1999 being larger and heavier (mean size  $\pm 1$  SE: 6.7 mm  $\pm 0.05$  for 1999, 5.9 mm  $\pm 0.05$  for 2000; mean fresh weight  $\pm 1$  SE: 0.12 g  $\pm 0.004$  for 1999, 0.09 g  $\pm 0.004$  for 2000;  $p < 0.0001$  for both t-tests). Among the intact fruits, the mature ones were slightly larger, but almost twice as heavy as the immature ones within any given year and when both years were combined (Table 3).

### Spatial dispersal patterns of intact fruits in number and size

Spatial dispersal patterns of the collected intact fruits with respect to distance from the focal trees and directions are depicted in Figures 3 and 4. Both figures show the dispersal patterns were similar for both years. Most of the intact fruits collected were deposited within a short distance ( $< 4$  m) of the focal trees, and they all followed a negative exponential curve. However, the end of some transects exhibited an upward tendency. Fruits were not deposited evenly in all eight directions, with more fruits being deposited on the upper left quadrant (Figure 4). This pattern matched the prevalent wind direction during the dispersal period. We thus fit a second order negative binomial model. The fitting results are summarized

in Table 4, and the fitted model is depicted in Figure 5. Judging from the goodness-of-fit statistic ( $\chi^2$  test;  $p>0.1$ ), the model fit was acceptable. The fitted curves overestimated the deposited fruit density within 1-m of the focal trees (especially in the N, NW and NE directions), but from 2-m outward, the model fitted the data well.

For the size of the collected intact fruits, we did not



**Figure 2.** Collection dates and frequency distribution of collected intact (both mature and immature) Taiwan sassafras (*Sassafras randaiense*) fruits for 1999 and 2000.

**Table 2.** Number of Taiwan sassafras (*Sassafras randaiense*) fruits collected in 1999 and 2000.

Tree	Year					
	1999		2000		Total	
	Intact <sup>a</sup>	Damaged <sup>b</sup>	Intact	Damaged	Intact	Damaged
1	106	394	40	250	146	644
2	61	103	66	491	127	594
3	72	138	87	206	159	344
4	105	158	16	43	121	201
5	39	22	58	38	97	60
Subtotal	383	815	267	1028	650	1843
Total	1198		1295		2493	

<sup>a</sup>Mature and immature fruits combined; <sup>b</sup>Damaged and dried fruits combined.



detect any statistically significant difference with respect to distance and directions (ANOVA,  $F_{2,44} = 2.23$ ;  $p=0.12$ ). We did observe that heavier intact fruits were deposited near the parents and at some distance away from the parents (Figure 6). A quadratic model with respect to distance was thus fitted, and the fitted model (ANOVA,  $F_{2,44}=5.48$ ;  $p=0.008$ ;  $R^2=0.2$ ) with its 95% confidence intervals is depicted in Figure 6.

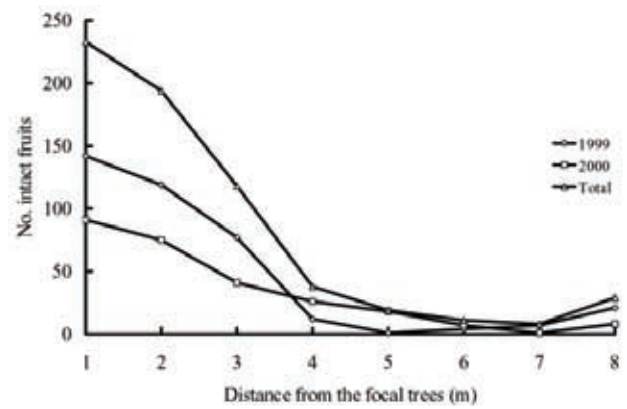
**DISCUSSION**

Similar to many previous studies on seed dispersal (e.g., Augspurger, 1983; Wenny, 2000b), the short-distance dispersal curve of Taiwan sassafras followed a negative exponential decline. Most of the intact fruits were deposited close to parents. But a slightly upward trend occurred at the end of the transect in certain directions. Such a trend allows some intact fruits to be deposited away from the immediacy, but still within the neighborhood, of the parents. Local environmental factors also played a role in shaping the spatial dispersal pattern (Westelaken and Maun, 1985). Being in the downslope directions and with the predominant wind during the summer mainly from the south and southeast, north-bearing directions received more intact fruits. Thus, the dispersal pattern of Taiwan sassafras was clearly anisotropic, a fact which might subsequently affect the next generation spatial structure. We did not detect any size difference with respect to distance and direction. For Taiwan sassafras, like many bird-dispersal species, fruit size is likely to be constrained by its long-distance dispersers (Jordano, 2000). Though the total numbers of fruits were about the same for both years, the proportion of mature fruits collected was higher in 1999. This temporal variation was due to the presence or absence of typhoons. During the dispersal season of 1999, no typhoon visited the study area. In contrast, in early July of 2000, a severe typhoon hit the study site directly and caused many fruits to fall before maturing (Figure 2).

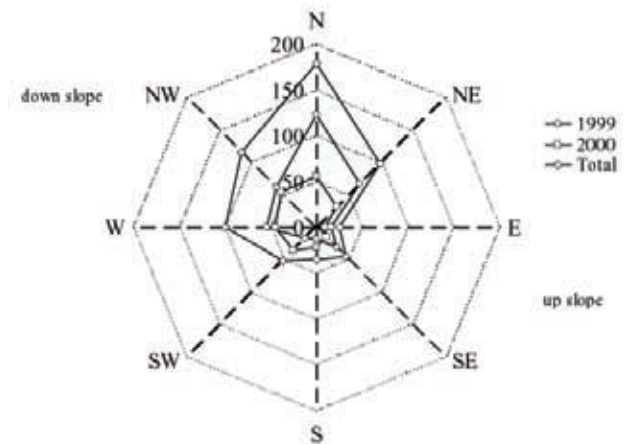
**Table 3.** Average size and fresh weight of mature and immature Taiwan sassafras (*Sassafras randaiense*) fruits collected in 1999 and 2000.

Year	Fruit type	Mean size ± 1 SE (mm)	Mean fresh weight ± 1 SE (g)
1999	Mature	6.99±0.07	0.16±0.007
	Immature	6.38±0.06	0.09±0.005
	Difference	0.61±0.09**	0.07±0.008**
2000	Mature	6.25±0.10	0.14±0.007
	Immature	5.77±0.06	0.07±0.004
	Difference	0.48±0.12**	0.07±0.007**
Combined	Mature	6.78±0.06	0.15±0.005
	Immature	6.08±0.04	0.08±0.003
	Difference	0.70±0.07**	0.07±0.06**

\*\* $p<0.0001$  based on t-test.



**Figure 3.** For the collected intact Taiwan sassafras (*Sassafras randaiense*) fruits, observed fruit dispersal patterns in number with respect to the distance from parents for 1999, 2000, and both years combined.

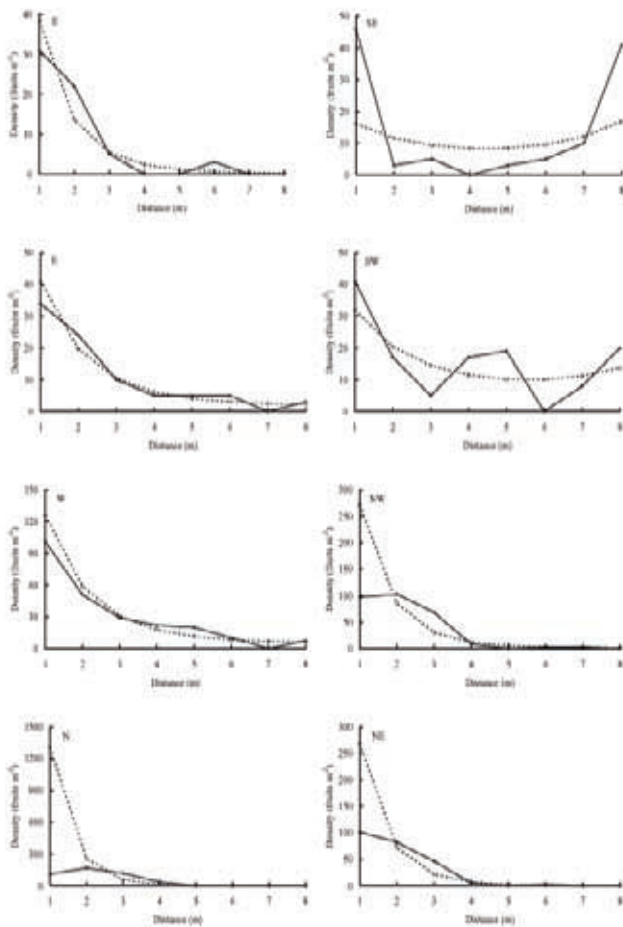


**Figure 4.** For the collected intact Taiwan sassafras (*Sassafras randaiense*) fruits, observed dispersal patterns in number with respect to the eight directions for 1999, 2000, and both years combined. For each direction, heavy dashed-lines represent the distance from the collection center, solid lines represent the number of fruits collected, and the light dashed-lines represent the number of fruits at a 50-fruit interval.

**Table 4.** Results of the likelihood ratio tests (Wald’s Type 3) of the fitted negative binomial model<sup>a</sup>. The dependent variable was the number of intact Taiwan Sassafras (*Sassafras randaiense*) fruits collected in 1999 and 2000, and the independent variables were direction, distance, and their interaction.

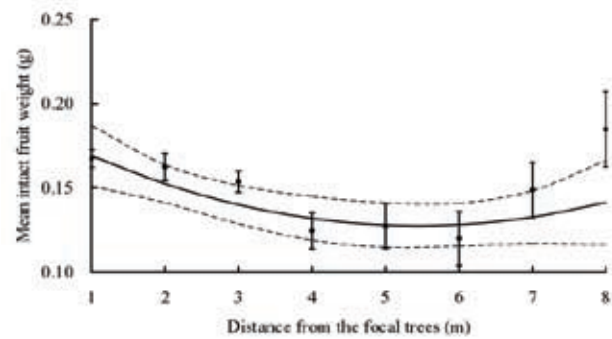
Source	DF	$\chi^2$ value (p-value)
Distance	1	20.73 (< .0001)
Direction	7	42.86 (< .0001)
Distance × Distance	1	4.25 (0.04)
Distance × Direction	7	51.48 (< .0001)

<sup>a</sup>Model overall deviance is 57.74 with  $df = 47$  and average deviance = 1.22; Pearson  $\chi^2$  is 52.26 with  $df = 47$  and average Pearson  $\chi^2 = 1.11$ .



**Figure 5.** Observed (solid line) and fitted (dashed line) fruit density (fruits  $m^{-2}$ ) with respect to the directions and the distance from the focal trees for the intact Taiwan sassafras (*Sassafras randaiense*) collected in 1999 and 2000.

Some studies have suggested that the amount of fruits and fruit weight are positively related to maternal size (tree height or DBH, e.g., Greene and Johnson, 1994), and the dispersal patterns are also significantly affected by maternal characteristics (e.g., Augspurger, 1983; Thiede and Augspurger, 1996; Peres and Baider, 1997). We did not detect such relationships in this study, except in 1999, when individual tree height had a significant and strong positive correlation with the total numbers of fruits collected. One possible explanation is the five trees all had an isolated and full crown, which probably means tree fruit production was not limited by scarce resources. The severe typhoon that occurred in early July of 2000 might also have caused the differences in fruit size and weight between the two years (Table 3). In addition, the spring of 1999 was the driest spring ever recorded in the study region, with only a quarter to one-third the normal precipitation. Whether that spring drought had any effect on fruit weight remains to be clarified. We could not offer any explanation why tree age had such a positive and significant correlation with the number of damaged fruits collected in 2000.



**Figure 6.** Observed (solid circle  $\pm 1$  SE) and fitted (solid line; together with a 95% confidence interval, dashed line) mean weight curves with respect to the distance from the focal trees for the intact Taiwan sassafras (*Sassafras randaiense*) fruits collected in 1999 and 2000.

Most of the heavier intact fruits that we collected were deposited close to the parents, likely due to gravity. However, some were also deposited beyond the crown (Figure 6), and we considered those fruits to have been dispersed by wind. Lin et al. (2003) found that in the study area, probably as an adaptation to low light availability in a cloud forest, the chlorophyll content of the outer portion of Taiwan sassafras crown is about 22% higher than the inner portion. Their findings suggest the outer portion of the crown could produce heavier fruits. Though the fruits matured, they were still light-weighted (averaged 0.15 g). With the help of frequent strong gusts during the summer, heavier mature fruits borne by the outer portion of the crown could thus have the opportunity to be dispersed away from the parents.

Our results suggest that typhoons could also affect the dispersal of Taiwan sassafras. Long-term records (from 1897 to 1996) show that about 1.4 typhoons per year hit the study site directly during the dispersal season. Depending on the timing, typhoons could potentially be both a positive and a negative factor. If a typhoon hits the study site in mid- to late-summer, the strong winds of typhoons could carry mature fruits away from the maternal trees. If a typhoon occurs in early summer, as in 2000, then most of the fruits will likely to fall prematurely, though the already matured ones could still benefit from the visit.

Although the germination rate of intact mature Taiwan sassafras fruits is low, such fruits might still contribute to maintaining the local population if they could counter the low germination rate by large numbers and could be dispersed away from the immediacy of their parents. At least for Taiwan sassafras, our results suggest that such a dispersal mode is possible. Existing literature on within-habitat dispersal of fleshy-fruited species rarely focuses on intact mature fruits and the role of wind in dispersing them. Our study suggests that both should deserve a closer look.

Because we did not monitor the fate of the dispersed mature fruits, our study could only indirectly support the

density-dependent hypothesis of Janzen-Connell and the escape hypothesis of Howe and Smallwood. If fruit weight has a positive effect on seedling emergence and survival ability as many studies have suggested (e.g., Wenny, 2000b; Cordazzo, 2002; Gómez, 2004), then our results agreed with the predictions made by the two hypotheses. Yet, heavier fruits (seeds) may not guarantee better germination success (Paz et al., 1999; Wenny, 2000b; Gómez, 2004).

Though only accounting for a minor portion among the fruits collected, digested fruits could be significant in maintaining the local population. Seeds from fruits consumed by animals usually have a higher likelihood of germination and survival (e.g., Wenny, 2000a; but see Wotton, 2002). The digested fruits that we collected could be from one of the focal trees or nearby trees as suggested by other studies (e.g., Wenny, 2000b), but they could also be from remote seed sources. We were unable to trace their origin.

This study was motivated by the observation that in the study region, once established, Taiwan sassafras can expand its population, become dominant, and maintain that dominance. We initially attributed such a phenomenon to clonal propagation (e.g., root suckering), as in American sassafras (*Sassafras albidum*) (Duncan, 1935). However, excavations of the sapling roots showed that this was not the case. Thus, an existing population has to rely on either a constant input of seeds via long-distance dispersal, or via short-distance dispersal from existing local individuals, or both, to maintain itself and expand. Two possible modes exist for short-distance dispersal, namely, by birds or possibly by wind. For the second mode to work, some quality intact mature fruits have to be deposited beyond the immediate vicinity of the parents. Results from this study suggest that for Taiwan sassafras the wind dispersal mode was indeed possible. Unquestionably, constant input of seeds from other areas can be an important source of recruitment too. We are currently conducting a fine-scale genetic analysis to determine the relative importance of the two possibilities.

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## 台灣東北部溫帶山區雨林內台灣檫樹完整果實之短距離分布

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本研究旨在探討台灣東北部棲蘭山區內台灣檫樹 (*Sassafras randaiense* Rehder) 完整果實之短距離分布特性，進而推論風力是否可能為該樹種果實潛在的傳播力量之一。研究於 1999 與 2000 年該樹種果實散播期間將蒐集網置於五株母樹下方，依八個方向蒐集由母樹中心至 8 公尺距離內之散播果實。而後分析所蒐集之完整果實其數目，大小，重量是否會依距離與方向之不同而異。結果顯示受損之果實佔全部所蒐集果實之 74%。在完整果實中，成熟果實之大小與未成熟者相似，然重量卻為後者之兩倍。此外本研究亦發現 (i) 大多數之完整果實均散播於母樹附近，(ii) 可能受地形與盛行風向之影響，較多之果實散播於北向坡，(iii) 各方向之果實數量散播曲線相似，(iv) 完整果實之大小不會依方向與距離之不同而有所差異，(v) 散播在母樹正下方與母樹冠層之外的成熟果實其重量較重。由所蒐集之完整果實在數量與重量之空間分布型式上觀之，除重力外，台灣檫樹亦可能利用風力進行短距離散播。

**關鍵詞：**不均勻傳播；漿質核果；台灣檫樹；風力傳播。