

# The essential role of tree-fern trunks in the regeneration of *Weinmannia tinctoria* in rain forest on Réunion, Mascarene Archipelago

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**Abstract:** The regeneration processes and the spatial distribution of the shade-intolerant *Weinmannia tinctoria* seedlings in the south of Réunion were investigated, with a special focus on the role of tree-ferns in seedling establishment. Mature individuals and seedling patches of *Weinmannia tinctoria*, and also tree-ferns, were mapped on two 1-ha rain-forest plots. *Weinmannia tinctoria* has hemi-epiphytic behaviour since seedlings were generally located on plant supports (99.6%). Regeneration was better on a support than on the ground, and germination tests showed that seeds were light-stimulated. Tall tree-ferns (*Cyathea* spp.) were suitable supports. *Cyathea glauca* and *C. excelsa* were more suitable supports than *C. borbonica*. *Weinmannia tinctoria* establishment complies with the facilitation model of succession and is dependent on tree-ferns.

**Résumé:** La régénération et la distribution spatiale des semis de *Weinmannia tinctoria*, espèce intolérante à l'ombre, ont été étudiées dans le sud de La Réunion. Nous nous sommes intéressés au rôle des fougères arborescentes sur l'émergence de plantules. Les adultes matures et les taches de semis (ensembles de plusieurs plantules) de *Weinmannia tinctoria*, de même que les fougères arborescentes, ont été cartographiés sur deux parcelles de 1 ha en forêt humide. *Weinmannia tinctoria* a un comportement héli-épiphyte car les semis se situaient principalement sur des supports (99,6%). La régénération se révélait meilleure sur les supports qu'au sol, et les tests de germination ont montré que les semences germaient mieux à la lumière. Les grandes fougères arborescentes (*Cyathea* spp.) constituaient des supports privilégiés. *Cyathea glauca* et *Cyathea excelsa* représentaient des supports plus favorables que *Cyathea borbonica*. *W. tinctoria* apparaît donc comme une espèce qui s'installe principalement en utilisant le modèle de facilitation et qui dépend de la présence de fougères arborescentes.

**Key Words:** colonization, ferns, germination, islands, montane forest, regeneration, seedlings, succession

## INTRODUCTION

The high level of small-scale heterogeneity in rain forests contributes to the local coexistence of species that share the same ecological niches in the adult stage but have different regeneration niches (Grubb 1977). The vegetation itself may create local conditions impacting on the regeneration of different species (Benítez-Malvido 2006, Male & Roberts 2005). The role of fallen trees on regeneration and seedling development has been highlighted in both temperate and tropical forests

(Brandani *et al.* 1988, Christie & Armesto 2003, Liao *et al.* 2003, Riera 1985). However, very few quantitative studies deal with regeneration using live plant supports, and only recent ones involve the role of tree-fern trunks in seedling establishment (Coomes *et al.* 2005, Mehltreter *et al.* 2005).

*Weinmannia tinctoria* Sm. (Cunoniaceae) is a common long-lived and emergent tree of the montane rain forest of Réunion (Scott 1997). The species frequently occurs as juvenile and mature trees in late-successional stands. It can therefore be expected that *W. tinctoria* uses specific regeneration mechanisms that allow it to regenerate in late-successional stands of Réunion montane rain forests. *Weinmannia racemosa* was observed regenerating

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on tree-ferns in New Zealand (Beveridge 1973, Wardle 1966), but the relative role of such living supports in the recruitment of *Weinmannia* has never been investigated in a quantitative way. In this study, we show the role of tree-fern supports in the regeneration of *W. tinctoria* in montane rain forest. Our work is based on the three following questions: (1) What are the regeneration patterns and the spatial distribution of *W. tinctoria* seedlings in rain forests? (2) Do the three native tree-ferns (*Cyathea borbonica* Desv., *C. excelsa* Swartz and *C. glauca* Bory) have a decisive role on the species regeneration? (3) How do tree-ferns of different species or size (diameter and height) classes determine *W. tinctoria* regeneration?

## METHODS

### Studied vegetation

Réunion (21°S, 55°30'E, 2512 km<sup>2</sup>) is a volcanic island of the Mascarene Archipelago in the south-western Indian Ocean (Figure 1). The species richness of the native flora is rather poor, consistent with the island's small size, but endemism is high, as 55% of the 486 flowering

plant species are endemic to the Mascarene Archipelago (Cadet 1980). The montane rain forest extends from altitude 800 m to 1900 m on the windward side and 1100 m to 2000 m on the leeward side (Strasberg *et al.* 2005). It is characterized by the richness of epiphytes and the abundance of tree-ferns. The dominant trees and shrubs of the native montane rain forest are *Aphloia theiformis*, *Doratoxylon apetalum* (Poir.) Radlk., *Homalium paniculatum* (Lam.) Benth., *Nuxia verticillata* Lam., *Syzygium cymosum* (Lam.) DC. and *Weinmannia mauritiana* D. Don (Tassin *et al.* 2004). The dynamics of native vegetation have been poorly documented (but see Strasberg 1995).

*Weinmannia tinctoria* is endemic to Réunion and Mauritius and is a common and even sometimes dominant species in montane rain forests of Réunion. This tree species can reach 15–20 m in height and 1 m in diameter. Fruits are capsules containing 2–10 small ellipsoidal seeds, 0.7 mm long, with loose pubescence (Scott 1997). About 9500 seeds are contained in a single gram.

### Study sites

Our fieldwork took place at two sites: the Rivière des Remparts and Bon Accueil (Figure 1). On each site, data were collected on a 1-ha square study plot. The site of the Rivière des Remparts is located on a recent basaltic flow from the Piton de la Fournaise volcano. The mean altitude of the study plot is 1630 m. Annual rainfall is 2100 mm (1974–2003) and mean annual temperature is 13.6 °C (1974–2003). The site of Bon Accueil is located on volcanic material from the Piton des Neiges volcano. The mean plot altitude is 1200 m. Annual rainfall is 2000 mm (1958–2004) and mean annual temperature is 16.8 °C (1958–2004). Soils are andisols on both sites (Raunet 1991).

### Data collection

The spatial distribution and the regeneration of *W. tinctoria* were studied on both plots. Each plot was divided into 100 quadrats measuring 10 m × 10 m to make data collection easier and more precise. Plots and quadrats were delimited using topographical thread and a bearing compass. Within each quadrat  $Q_i$ , all *W. tinctoria* and tree-fern specimens were mapped in  $X_iY_i$  coordinates, in order to deduce XY coordinates within the whole plot. The precision of X and Y was 0.1 m. Their height (H) and diameter at breast height (dbh) were recorded for individuals with dbh ≥ 8 cm. We defined a seedling as a young plant grown from a seed and not exceeding 20 cm tall, and a seedling patch as a group of seedlings growing

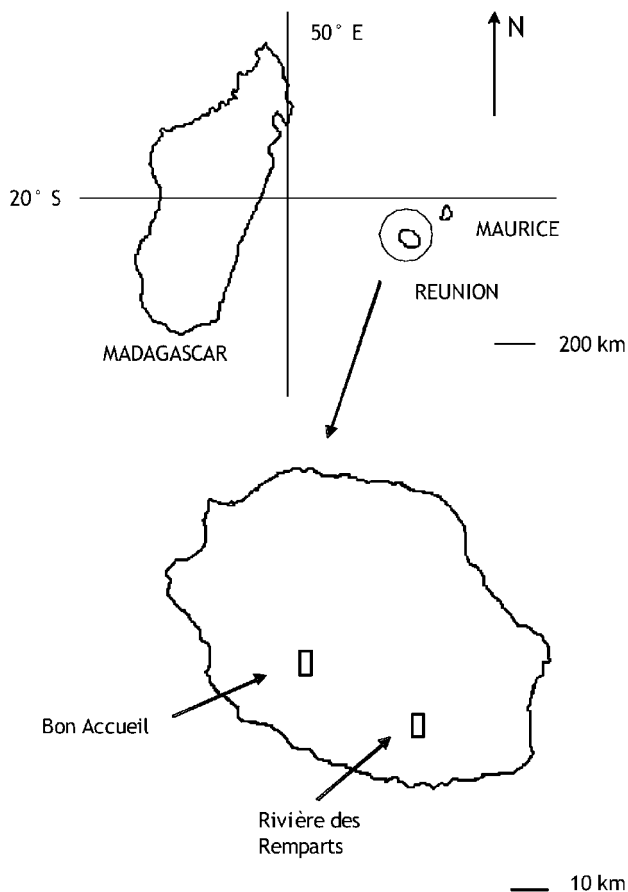


Figure 1. Location of the study sites.

on the same individual support or, if located on the soil, having the same XY coordinates. All seedling patches of *W. tinctoria* located on plant supports or soil were mapped. Within each patch, we counted the number of seedlings and recorded the microsite type (i.e. plant support or soil). When the support was vegetation, we also recorded the species of the plant support. The mapping of seedling patches was done quadrat by quadrat. We used measuring tapes and a bearing compass. Data collection was carried out in May 2003 at Bon Accueil site, and between July 2002 and April 2003 at Rivière des Remparts.

In the laboratory, germination tests were conducted to check that *W. tinctoria* produced light-stimulated seeds. They were performed in transparent Petri dishes placed in a germination cabinet at 15 °C (average condition on the distribution area of *W. tinctoria*). Two light treatments were tested: under constant light (under an illuminance of 2500 lx) and in the dark. Seeds were placed on sterilized sifted river sand. The sand was saturated with water using a sprayer. Each treatment was tested on four replicates of 25 seeds. The number of seeds that had germinated was regularly recorded until no more germination was observed. Germination was monitored over 45 d. It was defined as the appearance of the radicle (first seedling root).

### Data analysis

Relationships between spatial distributions of seedling patches and mature trees of *W. tinctoria* were analysed using the bivariate (intertypes) extension of Ripley's K function (Ripley 1977) as provided by Diggle (1983). It was used to test whether spatial distributions of two populations were dependent (i.e. showing aggregation or repulsion) or independent. We considered the individuals taller than 4 m as mature, since they were generally able to produce seeds (Rivière pers. obs.). Intertype analysis was carried out using the specific routines developed by Goreaud & Pélissier (1999) in ADE4 (Thioulouse *et al.* 1997). It was processed on the maximum value of 50 intervals with an interval length of 1 m. The maximal distance (50 m) is equal to half the size of a side of the plot. The method implemented for edge-effect correction in ADE4 does not allow computing the intertype function for larger distances than half the length of the longest side of a rectangle (Goreaud & Pélissier 1999), and other methods present the same limitation (Couteron & Kokou 1997).

Precision of the simulated coordinates to compute a local confidence interval was fixed at 0.1 m with 10 000 Monte Carlo simulations for a type one error of  $\alpha = 0.01$ .

In both sites, a Kolmogorov–Smirnov test confirmed that the distribution of the number of seedlings per patch was not normal, which justified the utilization of the Kruskal–Wallis (KW) non-parametric test. A KW test was

also used on germination results to test the effect of light. On each site and for different types of support, a KW test was also used between the number of *W. tinctoria* seedlings by tree-fern and the type of support to test the suitability of the support. This test was used for each tree-fern species (*Cyathea borbonica*, *C. excelsa* and *C. glauca*). The site effect was tested using the same KW test between the number of *W. tinctoria* seedlings by patch and the site (Bon Accueil and Rivière des Remparts). For Bon Accueil, a KW test was carried out between the number of *W. tinctoria* seedlings on a tree-fern and the height classes of a tree-fern and between the number of seedlings and the diameter class of a tree-fern. Height classes used were < 1 m, 1–2 m, 2–4 m and 4–8 m. Diameter classes were < 8 cm, 8–17.5 cm, 17.5–27.5 cm, 27.5–37.5 cm, 37.5–47.5 cm and 47.5–57.5 cm (adapted from diameter classes routinely used in French forestry). KW test was processed using SYSTAT.

### RESULTS

*Weinmannia tinctoria* seedlings were rarely isolated. Only 1.09% of seedlings in Bon Accueil and 4.25% of seedlings in Rivière des Remparts were isolated seedlings. At Bon Accueil, we counted 283 patches totalling 5547 seedlings. Seedling number per patch ranged from 1 to 533 with a median of 6. At Rivière des Remparts, we found 124 patches totalling a much lower number of 470 seedlings. Seedling number per patch ranged from 1 to 34 with a median of 2. The intertype spatial structure analysis carried out between mature trees and seedling patches of *W. tinctoria* showed that the spatial structure of mature trees and seedlings were independent, for both sites considered and for any lag-distance tested (1–50 m) (figure not represented). This analysis involved 120 mature trees at Bon Accueil and 131 ones at Rivière des Remparts.

KW test showed that light had a significant effect on germination ( $P = 0.018$ ). Mean germination after 43 d of incubation was 46% (SD = 5.2) with light and only 2% (SD = 4.0) in the dark. Beyond 43 d no more germination was observed.

Most of the seedling patches (99.6%) were located on a plant support. Only 0.7% of the patches at Bon Accueil were located at ground level. All the Rivière des Remparts patches were located on an elevated support. Supports could be tree-ferns (*Cyathea* spp.), living trees or dead trunks (Table 1). At Bon Accueil and Rivière des Remparts respectively, 90.5% and 58.3% of supports consisted of living and dead tree-ferns.

The KW non-parametric test carried out for each site showed a significant association between the number of seedlings and the type of structural support ( $P < 0.001$  at both sites). There was also a significant effect of site ( $P < 0.001$ ), with fewer seedlings by patch at Rivière des Remparts.

**Table 1.** Importance of the different types of supports for *Weinmannia tinctoria* seedling patches on both sites: number of patches on the considered support, percentage of the number of patches on the considered support compared with the total number of patches and number of individuals of the considered support species on the study site.

Supports	Bon Accueil			Rivière des Remparts		
	Number of patches	Percentage of the total	Number of individuals on the site	Number of patches	Percentage of the total	Number of individuals on the site
<i>Cyathea borbonica</i> Desv.	95	33.6	357	1	0.8	32
<i>Cyathea glauca</i> Bory	71	25.1	103	53	42.7	505
<i>Cyathea excelsa</i> Swartz	43	15.2	82	0	0.0	50
Dead tree-ferns	47	16.6		16	12.9	
<i>Monimia rotundifolia</i> Thouars	1	0.4	61	25	20.2	187
Dead <i>M. rotundifolia</i>	0	0.0		7	5.6	
<i>Aphloia theiformis</i> (Vahl) Benn.	2	0.7	1001	0	0.0	422
<i>Euodia obtusifolia</i> (DC.) T. G. Hartley	1	0.4	333	0	0.0	54
<i>Forgesia racemosa</i> J. F. Gmel.	1	0.4	39	5	4.0	146
<i>Hypericum lanceolatum</i> Lam.	1	0.4	111	0	0.0	63
<i>Weinmannia tinctoria</i> Sm.	1	0.4	540	0	0.0	318
Other dead trees	18	6.4		17	13.7	
At ground level	2	0.7		0	0.0	
Total	283	100		124	100	

At Bon Accueil, the KW test on tree-fern heights showed a significant association between the number of supported seedlings and the height class of tree-ferns ( $P < 0.001$  for the three species). Furthermore, there was a significant association between diameter class of a tree-fern and the number of seedlings it supported ( $P < 0.001$  for the three species). Tree-ferns were taller and bigger at Bon Accueil than at Rivière des Remparts: 47.0% of tree-ferns were taller than 2 m at Rivière des Remparts whereas 70.5% were at Bon Accueil.

## DISCUSSION

### *Weinmannia tinctoria* grows as a hemi-epiphytic species

The spatial patterns of *W. tinctoria* seedlings do not depend on those of the adults. They seem to result from the passive selection of seedlings which germinate and survive in microsites providing convenient conditions for seed germination (Willson & Traveset 2000). First, elevated supports allow the seedling to grow out of the herbaceous layer and thereby to receive more light (see Harmon & Franklin 1989 on *Picea-Tsuga* forests). Other results obtained on *Weinmannia racemosa* in New Zealand also showed that germination was inhibited in the dark and that seed germination was very poor on soil, indicating an intolerance of too much crowding (Burrows 1999). Consequently, the germination of *Weinmannia* spp. increases on elevated supports where light availability is usually higher than on the ground level and where competition is lower. Second, elevated supports prevent seeds from being buried under litter accumulation

which compromises the germination of small-sized seeds (Christie & Armesto 2003, Dalling & Hubbell 2002, Foster & Janson 1985, Lusk 1995, Nakashizuka 1989). It has been shown that seeds of *W. racemosa* do not germinate when buried (Burrows 1999).

*Weinmannia tinctoria* grows as a hemi-epiphytic species, i.e. a plant that is strictly epiphytic for only a part of its life as it germinates on a support and its roots penetrate the soil while growing (Puig 2001). Such observations have been reported for at least three other species within the genus *Weinmannia*: *W. trichosperma* in temperate humid forest of Chile (Christie & Armesto 2003), *Weinmannia racemosa* in New Zealand (Beveridge 1973, Coomes *et al.* 2005, Wardle 1966) and *Weinmannia* sp. in cloud forests of Costa Rica (Räber 1991).

### The role of elevated supports

Among the different types of support, tree trunks, and especially tree-fern trunks are the most frequent and the most suitable ones. Previous similar observations were recorded on *Weinmannia racemosa* in New Zealand which mainly regenerates on tree trunks (Beveridge 1973, Coomes *et al.* 2005, Wardle 1966) whereas the most common supports used by other species are dead trees (Christie & Armesto 2003, Harmon & Franklin 1989, Lusk 1995).

Trunk or stipe roughness of host plants is known as a main factor of variation in hemi-epiphyte distribution (Male & Roberts 2005, Patel 1996). The structure of tree-fern trunks appears to offer advantages for regeneration, maybe because of the adventitious roots (Newton &

**Table 2.** Number of seedlings (median and range) of *Weinmannia tinctoria* per tree fern according to the height and the diameter class of the tree-fern support for Bon Accueil site.

	<i>Cyathea borbonica</i>	<i>Cyathea excelsa</i>	<i>Cyathea glauca</i>
Height class (m)			
0–1	0 (0–1)	0 (0–0)	0 (0–0)
1–2	0 (0–2)	0 (0–0)	0 (0–0)
2–4	0 (0–18)	0 (0–68)	0 (0–61)
4–8	1 (0–32)	16 (0–136)	16.5 (0–533)
Diameter class (cm)			
0–8	0 (0–31)	0 (0–31)	0 (0–14)
8–17.5	2 (0–55)	5 (0–136)	4 (0–76)
17.5–27.5	0 (0–12)	19 (0–107)	17 (5–220)
27.5–37.5	–	13 (6–109)	43 (6–533)
37.5–47.5	–	23 (17–26)	–
47.5–57.5	–	19 <sup>1</sup>	–
Number of seedlings	574	1325	3129

<sup>1</sup> One individual in this class.

Healey 1989). Seeds can easily gain a hold at the level of persistent stipes and rachides of old fronds or between adventitious roots which are localized at the bottom of the trunk. The hairy tegument, also observed in other *Weinmannia* species, may be an adaptation to dispersal and facilitate the hold of the seeds (Webb & Simpson 1991). Moreover, light availability, but also organic matter accumulation from elevated litter and humidity along the tree-fern trunk is assumed to assure germination requirements.

Among the three tree-fern species growing on Bon Accueil, the more suitable ones are *Cyathea glauca* and *C. excelsa* (Tables 1 and 2). The higher density of adventitious roots they have on their trunk, compared with *C. borbonica*, might be a relevant explanation. Additionally, fronds of *C. glauca* fall during the dry season, which allow more light to penetrate the canopy and reach the seedlings. Such effects of vegetative phenology on seed germination have been previously recorded in a temperate forest (Seiwa 1998).

The size of tree-ferns strongly influences the establishment of seedlings. Almost no seedlings were found on tree-ferns smaller than 2 m tall and 8 cm in diameter, for the three species of *Cyathea*. Small tree-ferns do not have enough adventitious roots to enable regeneration of *W. tinctoria*. As tree-ferns are taller and bigger at Bon Accueil than at Rivière des Remparts, a larger number of suitable microsites improves germination success and seedling establishment.

### Facilitation effects of tree-trunks

*Weinmannia tinctoria* uses the model of facilitation defined as the modification by individuals of their environment in a manner that favours individuals with other life

history traits (Connell & Slatyer 1977, Huston & Smith 1987, Turner 1983). Facilitation by tree-ferns occurs through two different steps of *W. tinctoria* regeneration. First, during seed dispersal, tree-fern trunks act as seed-traps by helping the haired-seed to hold on an elevated support. Second, through seedling establishment, they provide water and organic matter and make access to light easier. Tree-ferns act as nucleus plants which ameliorate abiotic conditions for seedling establishment of *W. tinctoria* (Callaway 1995).

*Weinmannia tinctoria* is a long-lived and shade-intolerant emergent species producing light-stimulated seeds. Long life span and facilitation from tree-ferns enable it to persist in late-successional stages (Lusk 1999). Despite having characteristics of a gap-dependent pioneer species, e.g. small-sized and light-stimulated seeds (Fenner 1987, Huston & Smith 1987, Whitmore 1989), *W. tinctoria* is also able to regenerate and grow under closed canopy. *Weinmannia tinctoria* regeneration is easier in late-successional forests where seedlings can find more elevated supports. Our results suggest that the current distribution of mature individuals of *W. tinctoria* is determined by past tree-fern distribution and differential survival of seedlings.

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