# Seed Rain, Dispersal Distance, and Germination of the Invasive Tree *Spathodea campanulata* on the Island of Tahiti, French Polynesia (South Pacific)

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# Seed Rain, Dispersal Distance, and Germination of the Invasive Tree *Spathodea campanulata* on the Island of Tahiti, French Polynesia (South Pacific)[1]

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**Abstract:** The African tulip tree *Spathodea campanulata* is a major invasive species on the island of Tahiti (French Polynesia), where it has established from sea level up to montane cloud forest. This invader continues to spread across the island; however, little information is available about the seed rain and germination rate of *Spathodea* seeds. In this study, we quantified seed rain of *Spathodea*, estimated potential seed dispersal distances, and determined temperatures required for seed germination. Seed traps were positioned in a *Spathodea*-dominated forest and monitored over 86 days during the seed-fall period. The cumulative seed rain generated a density of 289 *Spathodea* seeds per square meter with a mean daily frequency of 3.3 seeds/m$^2$ in the plot. Based on seed production estimates from canopy pod counts, we inferred that many *Spathodea* seeds were dispersed away from the plot, rather than being deposited locally in the *Spathodea* invaded plot. A simple dispersal model indicated that seeds from a single tree perched on a steep precipice are capable of dispersing across the entire island of Tahiti during strong trade winds. Laboratory germination tests of freshly collected seeds showed that the maximum germination (100%) was obtained at 25 °C while 96% germination was observed at 20 °C; however, no germination was observed at 15 °C or 12 °C after 34 days. Thus, *Spathodea* invasion in Tahiti may currently be limited to elevations <1,500 m due to lack of germination at cooler temperatures. The large number of seeds per adult *Spathodea* as well as the seed dispersal ability and high rate of germination may provide an important establishment advantage to *Spathodea* in the tropical rainforests of Tahiti. We unexpectedly found that 61% of *Spathodea* seeds that fell in seed traps were depredated before falling in the traps. It is not known whether this predispersal seed predation has reduced *Spathodea*'s rate of spread in Tahiti.

**Keywords:** African tulip tree, biological invasion, Society Islands, seed dispersal

Many studies show that invasive plant species are continuing to spread at an alarming rate and cause major problems in natural ecosystems, especially on islands where they can threaten native species through competition, alter trophic interactions, and increase habitat fragmentation (e.g., Meyer 2004, 2014, Daehler 2005, Bramwell and Caujapé-Castells 2011, van Kleunen et al. 2015, Messerli and Larrue 2015, Russell et al. 2017). Therefore, invasive alien species have been identified as a key driver of change in native ecosystems (Vilà et al. 2011).

Due to geographic isolation and small land area, the remote Pacific Islands are particularly prone to invasive species (Keppel et al. 2014). The invasive evergreen tree *Spathodea campanulata* P. Beauv., 1865 (here after

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*Spathodea*), commonly called African tulip tree, is native to the Equatorial region of the west coast of Africa to Central East Africa (Irvine 1961). During the 20th century, *Spathodea* was introduced on many Pacific tropical islands where it became invasive in most of the high volcanic islands including the Cook Islands, Fiji, French Polynesia, Guam, Hawaiian Islands, New Caledonia, and Vanuatu (PIER 2011). *Spathodea* is observed in secondary forests (Bito 2007) and frequently established in the lowland tropics on deforested lands (Francis 2000), past human cultivated lands (Kress and Horvitz 2005), or on agricultural lands, where it is reported as a major problem for farmers (Labrada and Diaz Medina 2009). Furthermore, this invasive species is also reported in native closed forests, for example, in Cuba (Labrada and Diaz Medina 2009), in the Hawaiian Islands (Smith 1985, Staples and Cowie 2001), and in the Society Islands (Larrue et al. 2016).

In native forest, *Spathodea* is assumed to modify forest structure by reducing light incidence at the ground, leading to a decrease of understory native species richness (Weber 2003). Due to the wide ecological range of *Spathodea*, as well as the threat it may pose to native plants, this fast-growing tree is viewed as one of the world's worst invasive alien species (ISSG 2013).

In 1932, *Spathodea* was first introduced in French Polynesia to the island of Tahiti (Society Islands), where it was planted as an ornamental tree in a few locations on the coastal plain (Larrue 2008). It then spread in natural environment through wind dispersal. Due to its ecological plasticity (Florence 1997), including seedling shade-tolerance (Larrue et al. 2014), *Spathodea* has established in secondary and native forests of Tahiti, where it was reported as a major invasive tree in the 1980s (Fosberg 1992, Florence 1993). Since that time, *Spathodea* has been observed on the seven major high volcanic islands of the Society Islands and has been officially identified by the Government of French Polynesia as a species threatening native biodiversity (decree 244 CM of the 12 February 1998). On the island of Tahiti, this invasive tree is found in lowland mesic to moist rainforests, and in high-elevation native forests (montane cloud forest), where 63% of the endemic plant species are found (Meyer 2010).

It is well known that the invasiveness of introduced plants in new geographic areas may be related to possession of novel chemical traits as compared with the native flora in the introduction area (Callaway and Ridenour 2004) or competitive advantages under particular environmental conditions (Mooney et al. 2005). Additionally, wind dispersal of alien plant seeds also plays a key role in the invasion of natural habitats and predictions of wind dispersal distances are useful for knowing potential invasion ranges and rates (Egawa 2017). Following seed dispersal, the germination rate might also be important to explain invasion success.

Little information is available about wind dispersal distances, seed rain, and temperatures for germination of *Spathodea*, although this knowledge is crucial for understanding the tree's invasion potential. In this study, we quantified seed rain of *Spathodea* beneath established canopies and estimated the suitable range of temperatures for seed germination. Additionally, *Spathodea* seed dispersal distances were estimated with a simple model. We hypothesized that many *Spathodea* seeds disperse away from forests dominated by adult *Spathodea* and that germination rates of fresh seeds would be high in the tropical temperatures of Tahiti.

## MATERIAL AND METHODS

### *Study Species*

*Spathodea campanulata* (Bignoniaceae) is a large tree reaching 25 m in height with a dense crown (Smith 1985). It can reproduce via suckers, but it is mainly propagated by wind-dispersed seeds (Keay 1957, Staples et al. 2000). The seeds are contained in pods and each of them contains about 500 papery winged seeds (Fosberg et al. 1993). Morphological data and genetic matching demonstrated that *Spathodea* trees of the Pacific Islands originated from West Africa (Sutton et al. 2017), and therefore some West African arthropods might be identified and used as biological control agents in the Pacific Islands (Paterson et al. 2017).

The native range of *Spathodea* is localized in the African Equatorial region between 12° latitude South and North with a mean temperature about 27 °C (coldest month) and 30 °C (warmest month) (Francis 1990). No information is available about the range of rainfall in its native range. However, in its introduced range, *Spathodea* can survive with as little as 1,000 mm of annual precipitation and successful reproduction is observed with less than 1,300 mm of annual precipitation, but the most aggressive reproduction and growth was found between 1,600 and 2,000 mm of mean annual precipitation (referring to the island of Puerto Rico (Francis 1990)). Furthermore, *Spathodea* can survive on different substrates and slope steepness (Larrue et al. 2016) with both poor and excessive soil drainage (Florence 1997). At the forest floor, *Spathodea* seedlings tolerate different light environments (Larrue et al. 2014). In addition, *Spathodea* saplings show high photosynthetic rates from sea level up to, at least, 1,000 m elevation on Tahiti (Larrue et al. 2016).

### *Study Site*

In French Polynesia (South Pacific), *Spathodea* is particularly abundant on the high volcanic island of Tahiti (Society Islands), where the densest population is currently found on the northwest or leeward coast (Larrue 2008, Pouteau et al. 2015). Tahiti, located between 17° 29′ 50″–17° 52′ 32″ S and 149° 07′ 40″–149° 36′ 48″ W, is the largest and highest island of the Society archipelago with a land surface of 1,045 km$^2$ and 2,241 m maximum elevation (Brousse 1993). The field site is on the gentle slope of a forested gulch located at 149° 31′ 58.7712″ W–17° 33′ 46.8936″ S and 404 m elevation in the valley of Hamuta (Pirae district) on the leeward coast of Tahiti (Figure 1).

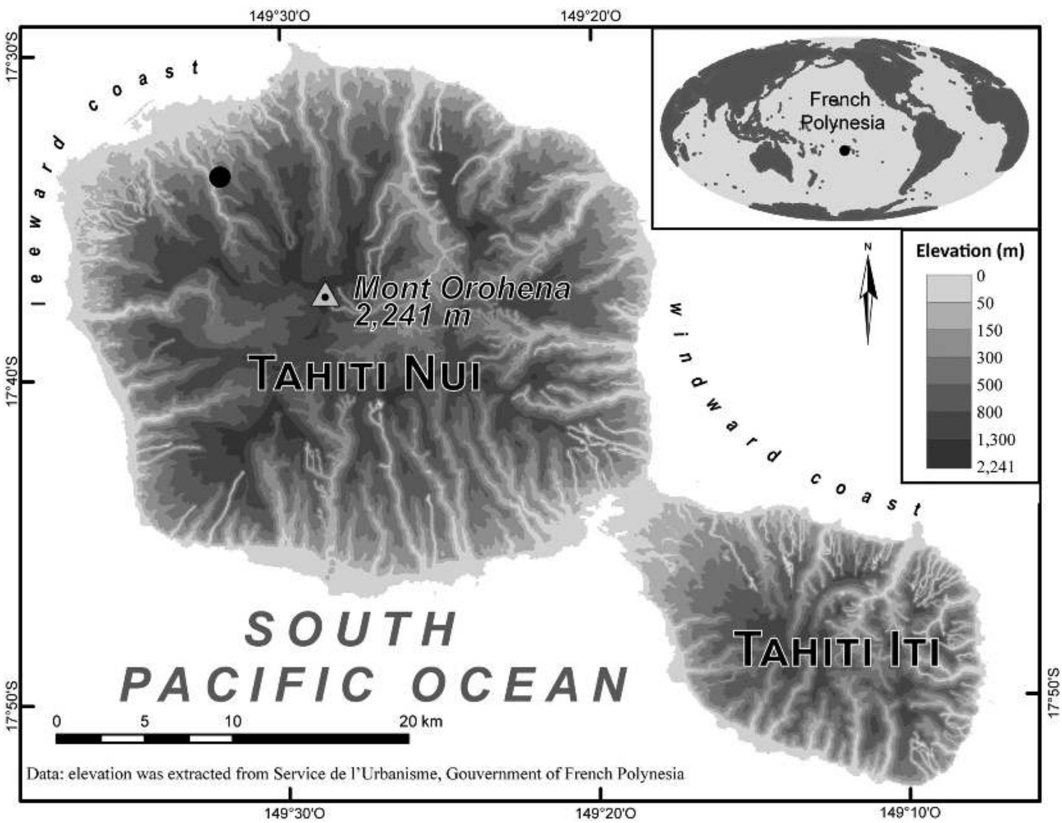


FIGURE 1. Study site. Location of the circular plot (black circle) with seed traps on the island of Tahiti (Society Islands, French Polynesia).

TABLE 1

List and Abundance (% Cover) of the Vascular Plant Species Observed in the 177 $m^2$ Plot According to Forest Strata

| Plant Species ($n = 18$) | Plant Family | Biogeographic Status | Forest Stratification | | |
|---|---|---|---|---|---|
| | | | Tree Layer | Shrub and Vine Layer | Herb and Fern Layer |
| Dominant species: | | | | | |
| *Spathodea campanulata* P. Beauv. | Bignoniaceae | Eur | 50–75% | 1–5% | 1–5% |
| *Syzygium cumini* (L.) Skeels. | Myrtaceae | Eur | 5–25% | 1–5% | 1–5% |
| *Ardisia elliptica* Thunb. | Myrsinaceae | Eur | – | >75% | >75% |
| Other species: | | | | | |
| *Adenanthera pavonina* L. | Fabaceae | Eur | – | <1% | 1–5% |
| *Adiantum trapeziforme* L. | Adiantaceae | Eur | – | – | <1% |
| *Coffea arabica* L. | Rubiaceae | Eur | – | – | <1% |
| *Crepidomanes* sp. | Hymenophyllaceae | Ind | – | – | <1% |
| *Cyclophyllum barbatum* (G.Forst.) N. Hallé & J. Florence | Rubiaceae | Ind | – | – | <1% |
| *Dioscorea* sp. | Dioscoraceae | Pol? | – | – | <1% |
| *Mangifera indica* L. | Anacardiaceae | Eur | 1–5% | – | – |
| *Miconia calvescens* DC. | Melastomataceae | Eur | – | – | <1% |
| *Microsorum commutatum* (Blume) Copel. | Polypodiaceae | Ind | – | – | <1% |
| *Phyllanthus manono* Baill. ex Müll.Arg. | Phyllanthaceae | End | – | <1% | <1% |
| *Pimenta dioica* (L.) Merr. | Myrtaceae | Eur | – | 1–5% | 1–5% |
| *Plerandra elegantissima* (Veitch ex Mast.) Lowry, G.M. Plunkett & Frodin | Araliaceae | Eur | – | <1% | – |
| *Swietenia* sp. | Meliaceae | Eur | – | <1% | – |
| *Triplaris weigeltiana* (Rchb.) Kuntze | Polygonaceae | Eur | 1–5% | 1–5% | 1–5% |
| *Zingiber zerumbet* (L.) Roscoe ex Sm. | Zinziberaceae | Pol | – | – | 1–5% |

Species biogeographic status: European introduction (Eur), Polynesian introduction (Pol), indigenous (Ind), and endemic to the Society Islands (End). sp: unidentified species (no flower or fruit).

The mean annual temperature of Tahiti is 25.9 °C with a mean annual rainfall of 1,715 mm at sea level (https://en.climate-data.org) reaching 3,214 mm at 1,441 m (Mt Marau) and more than 10,000 mm per year above 2,000 m elevation (Dupon et al. 1993). The oceanic tropical wet climate of Tahiti is dominated by the influence of the south-eastern trade winds including two seasons: a warm wet season (November to April) with high atmospheric humidity (>90%), higher rainfall, and average monthly temperature of 26.7 °C; and a cooler season (May to October) with lower atmospheric humidity, reduced rainfall, and average monthly temperature of 25.1 °C (Laurent et al. 2004, https://en.climate-data.org).

### *Monitoring Seed Rain of* Spathodea

*Spathodea* seed rain was monitored using 16 seed traps from September to December 2019, while mature pods were releasing seeds. Seed traps were positioned in a circular plot of 177 $m^2$ within the midelevation secondary rainforest dominated by large *Spathodea* trees over 20 m tall (>50–75% canopy cover), with other naturalized alien trees such as the Java plum *Syzygium cumini* (>5–25%), the mango tree *Mangifera indica* and *Triplaris weigeltiana* (>1–5%). The understory was dominated by the invasive shrub *Ardisia elliptica* (Table 1; Figure 2*A*,*B*). The field site was chosen using three criteria: a forest dominated by mature *Spathodea* with pods; a relatively flat topography to allow easy establishment of a

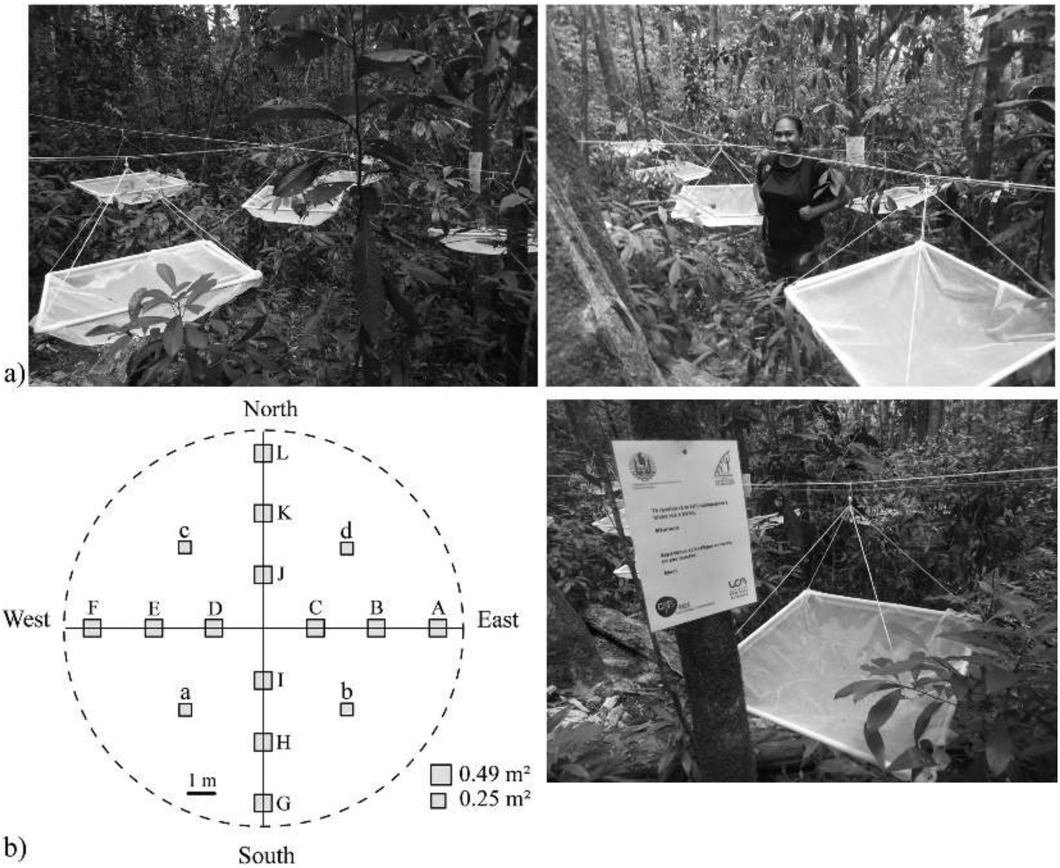


FIGURE 2. (*A*) General view of the seed traps in the field. (*B*) Aerial view of the seed traps (gray squares) pattern with positions of traps within the 177 $m^2$ circular plot (dashed circle line) and information panel on the island of Tahiti (Society Islands).

regular spatial pattern of seed traps; and easy accessibility of the site to visit traps regularly. The plot was also chosen to be representative of *Spathodea*-invaded forest in Tahiti in terms of *Spathodea* adult tree density.

Hanging mesh traps is a common approach to estimate seed dispersal in tropical forests (see Stevenson and Vargas 2008). Accordingly, seed traps consisted of 16 open quadrats constructed of PVC pipe loosely underlain with mosquito netting, to create a mesh trap with a depth of 30–40 cm in the center (Figure 2*A*). Traps were suspended ~1.3 m above the ground. Hanging mesh traps were two different sizes: twelve quadrats of 0.49 $m^2$ (70 × 70 cm) and four quadrats of 0.25 $m^2$ (50 × 50 cm) each. The twelve 0.49 $m^2$ seed traps were hung every 2 m along two perpendicular lines. The lines were oriented from north to south and east to west, delineated in a cross shape. We used this shape to uniformly cover each geographic compass orientation in the plot (Figure 2*A*,*B*), as compass orientation might be important to wind dispersed species when there are prevailing wind patterns. The four 0.25 $m^2$ seed traps were added side by side of the crossing lines. The total area of seed traps was 6.88 $m^2$. The traps were visited every 3–4 days from September 6 to December 4, encompassing a main period of seed release from maturing pods.

To check for seed predation in the traps, some seeds were marked slightly with a pen

TABLE 2

Characteristics of *Spathodea* in the 177 m$^2$ Plot, with the Number of *Spathodea*, the Number of Seeds per Seed Trap and Square Meter, and Total Number of Seeds in the Plot (Tahiti, Society Islands)

| *Spathodea campanulata* ($n = 23$) | Range | Mean Value | Total |
|---|---|---|---|
| Tree characteristics | | | |
| DBH (cm) | 10.8–55.7 | 24 | 650 |
| Basal area (m$^2$) | 0.0092–0.2437 | 0.05 | 1.51 |
| No. of visible pods per tree | 0–28 | 6.1 | 141 |
| No. of estimated seeds per tree[a] | 0–14,000 | 3,074 | 70,700 |
| Seed traps and plot | | | |
| No. of seeds per seed trap | 50–224 | 124.3 | 1,991 |
| No. of seeds (per m$^2$) | – | – | 289.4 |
| No. of seeds in the 177 m$^2$ plot | – | – | 51,223 |

Note that the number of visible pods and reported values represent a low estimate of the total number of pods and seeds, as the top of the tree canopy was only partially visible.

[a] The number of estimated seeds was empirically calculated with 500 seeds × No. of visible pods of the tree canopy in the plot.

and left in the traps for the next visit (i.e., 3–4 days). This marking experiment was conducted three times. To avoid possible vandalism of seed traps by people, information panels were included in the circular plot (see Figure 2*A*,*B* for an overall view).

To provide additional information about the plot environment, Diameters at Breast Height (DBH) of *Spathodea* trees were measured in the field and basal area was calculated. We also counted the number of visible *Spathodea* pods in the forest canopy and estimated the total number of available seeds that could potentially be dispersed (Table 2).

### *Seed Dispersal Distance from Release Point*

The simple model of Pasquill and Smith (1983) was used to provide an estimate of the horizontal distance that *Spathodea* seeds could be carried by the wind following the equation:

$$x = \frac{Hu}{F},$$

where $x$ is the predicted horizontal distance from maternal tree to the seed deposition site, $H$ is the release height above the ground (i.e., it may be from a tree at sea level and tree on steep precipice at high elevation as it is commonly observed on Tahiti (Figure 3*A*,*B*)), $u$ is the horizontal wind speed (m/s) between $H$ and the ground, and $F$ is a constant descent of the seed (i.e., velocity). $F$ is calculated by dividing $H$ (m) by the time (s) of flight of seed from the release elevation to the ground. The mean value of $F$ for *Spathodea* seeds was recorded as 0.378 m/s with SD 0.069 (mean of 250 seeds dropped at 3.65 m elevation in closed environment, i.e., under windless conditions).

To ensure the model provides a suitable prediction for the *Spathodea* seed dispersal distance, seeds ($n = 50$) were released in a flat open area (soccer field) at 2 m height above the ground. We measured the wind speed (m/s) with a handle anemometer (AM4220) and the distance to deposition site for each release of seed. We then used Spearman's correlation and a Wilcoxon–Mann Whitney test to compare the predicted dispersal distance (model) with the observed dispersal distance (measurements).

### *Germination Tests*

*Spathodea* seeds were pooled from three mature pods collected from three adults (i.e., one pod per adult tree) on Tahiti. The adults *Spathodea* were located in the valley of Hamuta (but not in the circular plot). A total of 180 seeds were extracted by random methodology and transported to the lab for germination tests. Seed germination of *Spathodea* was recorded at six constant tem-


FIGURE 3. (*A*) *Spathodea* at 750 m elevation on the leeward coast of Tahiti. (*B*) Example of some *Spathodea* identified with binoculars on steep precipice (>70°, see also Larrue et al. 2016) ~900 m elevation in the valley of Punaruu on Tahiti.

peratures of 12, 15, 18, 20, 25, and 30 °C with 12 h day light (solar spectrum 300–1,000 nm) in an ARALAB climatic chamber. These six temperatures were selected according to the mean annual temperature observed at different elevations on Tahiti.

A set of 30 *Spathodea* seeds was tested for each temperature. Each set of seeds was put in a plastic petri dish on a filter placed onto 0.5 cm depth moistened vermiculite. Petri dishes were sealed with parafilm to ensure saturated relative humidity for optimal seed germination. Seed germination (i.e., radicle emergence) was monitored every day over 34 days. Seeds not germinated at the end of the period were crushed to visually check their viability (i.e., observation of a living white embryo). The germination rate was calculated based on the number of viable seeds per set. Then, Fisher's exact test was used to compare if germination rate among these temperatures was statistically different.

## RESULTS

### *Seed Traps*

A total of 1,991 *Spathodea* seeds were collected from traps over 86 days (Table 2). *Spathodea* seeds collected in the 0.49 $m^2$ and 0.25 $m^2$ traps ranged from 104 to 224 and 50 to 120, respectively (Figure 4). *Spathodea* seed rain increased from September to October (peak of seed rain) and decreased in December. *Ardisia* seeds were also found in the traps in September, reaching a maximum number of seeds at the end of September (Supplementary Online Figure S1). A few undetermined seeds were also found throughout the study (Supplementary Online Figure S1).

The cumulative seed rain generated a density of 289.4 *Spathodea* seeds per square meter in 86 days with a mean daily seed rain density of 3.3 seeds/$m^2$. Accordingly, the total *Spathodea* estimated seed rain in the 177 $m^2$ plot reached 51,224 seeds and an average number of 2,227 seeds on the ground per *Spathodea* tree (Table 2).

No seed predation was observed on marked seeds left in the traps. However, 61% of *Spathodea* seeds found in the traps were damaged by predators in the tree canopy before falling in the traps. Thus, only 39% of the total *Spathodea* seeds found in the traps were viable (Supplementary Online Figure S1) leading to a cumulative density of viable seeds of 114/$m^2$ with a low mean daily seed rain density of 1.3 viable seeds/$m^2$.

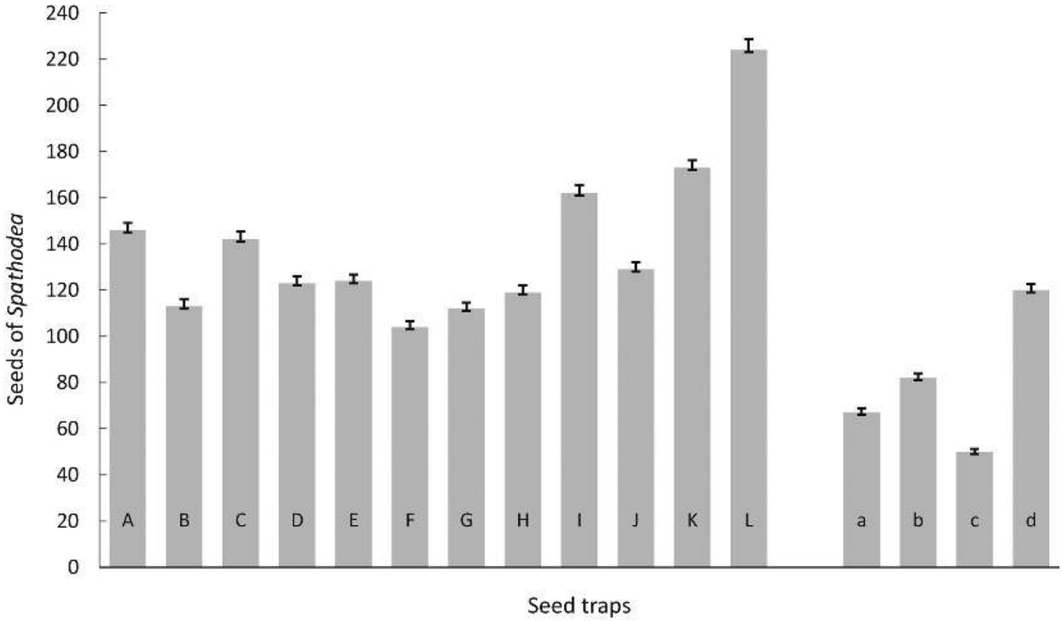


FIGURE 4. *Spathodea* seed rain collected over 86 days in each trap with twelve 0.49 $m^2$ traps (uppercase; standard deviation (SD) of seeds trapped = 32) and four 0.25 $m^2$ traps (lowercase; SD of seeds trapped = 25). Letters refer to the location of seed traps in the plot (see Figure 2*A*,*B*). Error bar refers to SD per seed trap.

### *Seed Dispersal Distances*

The predicted dispersal distances with the model were correlated with the measured dispersal distances (Spearman correlation, $r$s = 0.746; $P < 0.001$) and these values did not differ significantly (Wilcoxon–Mann Whitney test; $P$-value > 0.15). Thus, the model of Pasquill and Smith (1983) provides a relevant prediction for *Spathodea* seed dispersal distances (Figure 5). According to the model, Table 3 gives some seed dispersal distances from adult *Spathodea* at sea level and from its highest elevation, with different wind speeds commonly observed on Tahiti. These findings demonstrate that a typical adult tree

TABLE 3

*Spathodea* Seed Dispersal Distances from the Height of an Adult Tree (20 m) at Sea Level and from the Highest Elevation Site where Adult *Spathodea* is found on Tahiti (1,415 m) Considering Different Wind Speeds Observed in Tahiti

| Range of Wind Speed (m/s) | Month %[a] | | | | Dispersal Distance to the Deposit Site (m) from an Elevation of: | |
|---|---|---|---|---|---|---|
| | Sept. | Oct. | Nov. | Dec. | 20 m | 1,415 m |
| Trade winds | | | | | | |
| 0.01–0.5 | 26 | 26 | 24 | 20 | 0.5–26.4 | 37.4–1,871 |
| 0.6–3.6 | 57 | 58 | 60 | 59 | 31.7–190.4 | 2,246–13,476 |
| 3.7–11.3 | 17 | 16 | 15 | 21 | 195.7–613.7 | 13,850–42,300 |
| Cyclones (scale 1 to 3)[b] | | | | | | |
| 32.7–49.4 | – | – | – | – | 1,730–2,613 | 139,253–184,923 |

[a] Percentage of the wind in this range of wind speed per month on Tahiti (adapted from Laurent et al. 2004).
[b] Cyclonic intensity did not exceed Saffir-Simpson Hurricane Wind Scale 3 on Tahiti (Larrue and Chiron 2010).

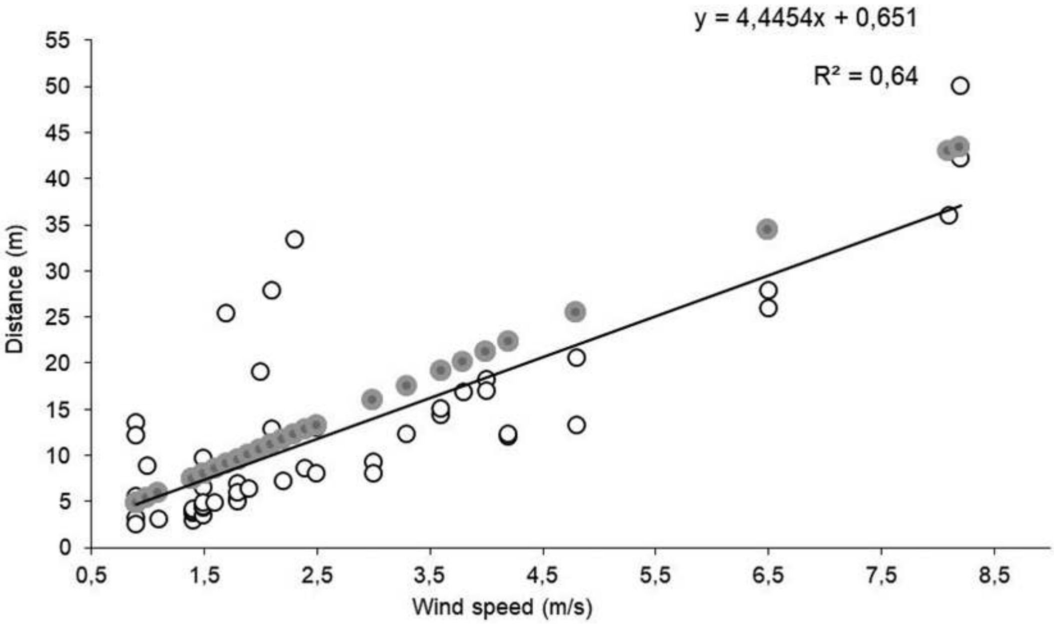


FIGURE 5. Predicted *Spathodea* seed dispersal distance (gray circle) with the model of Pasquill and Smith (1983) and observed dispersal distance (white circle) according to wind speed. Linear regression ($R^2$) refers to the observed dispersal distances *vs* wind speed values.

growing on a steep precipice can potentially disperse seeds across the entire distances of Tahiti (~32 km island diameter) assuming strong trade winds and unimpeded wind flow.

### *Germination Rate*

The maximum germination was obtained at 25 °C with a success of 100% in 9 days, while we observed 96% germination at 20 °C and 30 °C; the germination rate among these three temperatures was not statistically different (Fisher exact test, $P > 0.05$). The germination at 18 °C was slower (first germination at 14 days), with only 59% germination success after 27 days (Figure 6), and the germination rate at 18 °C was significantly lower than the germination rates at the three

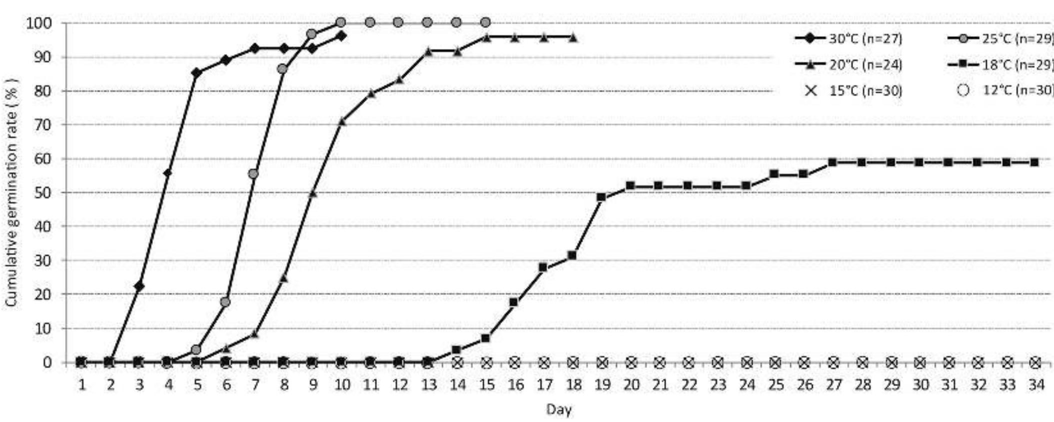


FIGURE 6. Germination rate of *Spathodea* seeds at different temperatures (°C) ranging from 12 °C to 30 °C monitored in the lab over 34 days. Bracket refers to the number of viable seeds used to build germination curves.

higher temperatures (Fisher exact test, all $P < 0.01$). No germination was observed at 15 or at 12 °C (Figure 6).

## DISCUSSION AND CONCLUSIONS

Based on our seed trap results and the number of mature trees in our plot, we estimated ~2,224 seeds were dropped into the plot per adult *Spathodea* tree. Considering our estimate of 6 mature pods per tree (Table 2) and 500 seeds per pod, this indicated that at least 25% of seeds dispersed away from the plot. This could be a dramatic underestimate given that not all pods on trees were visible (pod numbers are underestimates) and some seeds caught in traps likely originated from outside of our plot. Given that mature *Spathodea* may produce many pods in the fruiting season (i.e., 8 to around 100 pods thus giving 4,000 to 50,000 seeds per tree, Larrue, pers. obs), our findings suggest that thousands of *Spathodea* seeds are wind dispersed away from the plot, rather than being carried just a short distance, and deposited beneath the canopy or in the local vicinity. This result is in agreement with a study reporting that "*S. campanulata* is able to overcome the barrier effect of big trees present in the ecotone to spread its seeds" (Labrada and Diaz Medina 2009). Thus, wind dispersal of *Spathodea* seeds appears to be effective even when the trees are embedded in a dense forest matrix.

Figure 5 and Table 3 show that the dispersal distance from the release point depends on wind speed. Thus, most seeds found in the traps can be explained by lower wind speed (i.e., <0.5 m/s) leading to a dispersal distance ranging from 0.5 to 26 m (Table 3). This lower wind speed represents 20–26% of wind commonly observed on Tahiti between September and December (Table 3), although such low wind speeds may be more frequent within a dense forest canopy. Given that most of the time (up to 74–80%) trade wind is above 0.5 m/s on Tahiti, this suggest that most *Spathodea* seeds are wind dispersed in a range distance of 31 to more than 42,000 m, depending on the release height (see Table 3). In Tahiti, we observed *Spathodea* seeds on the ground in native forests up to 2,066 m (Mt Aorai) and 2,110 m elevation (Mt Pito Iti), more than 1.5 km distance as the crow flies from nearest adult trees (according to the map of Pouteau et al. 2015). Thus, *Spathodea* seeds can reach remote native forests on Tahiti, and this dispersal ability contributes to a wide infestation of the island.

The germination rate of *Spathodea* seeds was very high under 20–30 °C, with a maximum at 25 °C. This temperature is similar with the mean annual temperature of Tahiti. So, climate conditions in Tahiti are suitable for maximum germination of *Spathodea* seeds, especially during the warm and wet season following seed dispersal. Knowing that environmental lapse rate is 0.0063 °C $m^{-1}$ on Tahiti (Pouteau et al. 2010) and considering a minimum daily temperature of >15 °C required for *Spathodea* seeds germination, the current upper limit for germination in the wet season at the overall island scale should be below 1,800 m. More closely, temperature sensors set up in the 2013–2014 year on an elevation gradient on the leeward coast of Tahiti (Mt Aorai) indicated a mean annual temperature in forested gulches of 17.5 °C at 1,200 m and 14.6 °C at 1,700 m asl (J.-Y. Meyer, unpub. data). These measurements are congruent with field observation, where we found adults and *Spathodea* seedlings up to 1,415 m elevation on the west leeward coast of Tahiti (Mt Marau). According to Laurent et al. (2004), global warming has increased mean annual temperature by 0.0343 °C per year on Tahiti. Consequently, the upper limit of *Spathodea* invasion might be higher in the future.

The large number of seeds per adult *Spathodea* as well as their strong dispersal ability and high rate of germination may provide an important establishment advantage to *Spathodea*, helping it to reach new sites where it can successfully germinate and become established. Additionally, *Spathodea* seedlings can grow in closed forests with low light environments, for example, *Spathodea* seedlings were frequently observed under canopy in the range around 50 to 200 μmol photons $m^{-2} \cdot s^{-1}$ PAR (i.e., 2.5% to 10% of full sunlight) with maximum photosynthesis occurring at less than 13% of full sun (Larrue et al. 2014). Although we do not have measurement of growth of *Spathodea* compared to other neighboring native species, there is no doubt that it is a fast-growing tree, as young saplings can grow more than 2 m per year at sea level on Tahiti (Larrue, pers. obs).

An interesting finding of this study is that 61% of *Spathodea* seeds trapped were eaten in pods before falling in the traps. This predispersal seed predation was unexpected, and the identity of the predispersal seed predator was not confirmed. However, some observations in the field led us to consider the Common waxbill *Estrilda astrild* L. or *Neochmia temporalis* Latham, two small birds introduced to Tahiti in the early 20th century (Thibault and Cibois 2017), as possible predispersal seed predators. If seed predation rates become sufficiently high and consistent, this could potentially become a form of inadvertent biological control in Tahiti.

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