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Attributes of Naturally Fallen (Rained) *Melaleuca quinquenervia* Seeds in Two Habitat Types of South Florida Wetlands

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Abstract

Melaleuca quinquenervia is an Australian tree that has successfully invaded many habitats in Florida. It maintains an aerial seed bank in serotinous capsular fruits held in the tree canopies. These fruits open gradually and shed seeds that fall (rain) throughout the year. Comparative attributes (quantities and qualities) of these fallen seeds from different habitats and tree size categories are unknown. We documented these attributes of fallen *M. quinquenervia* seeds for 12 months among three tree size categories from each of the two hydrologically delineated habitat types. Quantities (8961 seeds $m^2 \cdot mo^{-1}$) and the viability (8.8%) and germinability (8.4%) of fallen melaleuca seeds in the occasionally inundated habitat were significantly higher (P = 0.05) than the quantities (6716 seeds $m^2 \cdot mo^{-1}$), and viability (5.6%) and germinability (5.3%) of melaleuca seeds in the permanently inundated habitat. Although relatively more seeds rained from larger trees, higher quality seeds were rained from the trees of smaller dimensions. Smaller trees typically inhabit at the edges of melaleuca stands and hence they may increase the potential for further spread of seeds into the adjacent areas.

Keywords

Exotic Invasive Tree, Habitat, Seed, Germinability, Viability, Quantity

1. Introduction

Melaleuca quinquenervia (Cav.) Blake (melaleuca) is an exotic tree of Australian origin. It has invaded ecologically sensitive wetlands in the Florida Everglades and other surrounding ecosystems that range from pine-palmetto uplands to permanently flooded water conservation areas. Introduced in the late 1880s [1], melaleuca has displaced native flora, reduced wildlife habitat, increased fire hazards, and exacerbated human health problems in Florida (e.g., [2] [3]). High reproductive capacity, superior competitive ability due to morphological or physiological plasticity, and rapid growth potential under multiple environmental conditions are often cited characteristics of invasive plants (e.g., [4] [5] [6] [7]) and melaleuca trees in Florida possess many of these invasive traits (e.g., [2] [8] [9] [10]).

High probabilities of seed dispersal, viability and germination enhance melaleuca's ability to colonize diverse habitats [4]. Melaleuca trees can become reproductive as early as one year after germination, and flowering events may repeat several times a year [8]. Inflorescences develop into the infructescence (capsule clusters) composed of 30 to 70 (mean 49 ± 17) sessile woody capsules each of which contain 200 - 350 seeds (e.g., [8] [11]). These capsules may remain attached to the trunks, branches, or twigs for up to 7 years or sometimes more. Hence the trees are serotinous in nature [8], bearing one to several capsule cohorts (cluster) at any given time [11]. These capsular fruits open when their vascular connections are disrupted by increased bark thickness or other stress factors such as fire, frost, mechanical damage, herbicide treatments, or self-pruning of branches (e.g., [2] [9]).

Seed production by melaleuca trees and their germinability has been noted to be site (habitat) specific [4]. Mature melaleuca tree stands have been reported to produce and retain a large amount of seeds (up to 550 $kg \cdot ha^{-1}$) in seed capsules held in the canopies for years [12]. A massive synchronous seed release and fall (rain) may occur from these canopy reservoirs following some sudden stresses such as forest fire, seed capsules normally open successively in a non-synchronous manner resulting in a light but constant seed rain (e.g., [2] [9]). In an earlier study, Woodall (1982) [9] reported individual tree based seed rain of 29 seeds $m^{-2} \cdot d^{-1}$. These differences in rates of seed rain may indicate inherent variability in the volume of melaleuca seedfall, both in time and space. Under wet conditions, most melaleuca seeds germinate within 10 days, although a small fraction of viable seeds may remain dormant [10]. In a similar study, Van *et al.* (2005) [13] reported that air dried seeds extracted from healthy mature seed capsules maintained 14% - 16% viability and 14% germinability for 7-yr when stored at room temperature. Conversely, the same seeds buried at 0.5 to 5 cm depth retained viability up to 1.5 and 2.3 years in wet and dry sites, respectively [13]. Even though no statistical difference was detected in the overall viability (8% - 9%) and germinability (6% - 8%) of composite seeds extracted from all ages of canopy-held capsulecohorts from occasionally and permanently inundated sites; a trend of low viability and germinability of seeds was observed in permanently inundated sites compared to those from occasionally inundated sites [10]. The overall viability and germinability of seeds retained in canopy held seed capsules peaked among middle age cohorts and decreased towards proximal and distal ends of infructescence bearing stems [10]. Overall, melaleuca's reproductive behavior and environmental plasticity comports well with its invasive nature.

The aforementioned research confirms melaleuca's massive seed producing ability and its resultant canopy-held seed reservoirs. Any negative impact on the overall quantity and quality of canopy-held melaleuca seeds via chronic damage of foliage, flowers or fruits is expected to suppress the invasive attributes of this exotic tree. Introduced melaleuca biological control agents have been proposed to have such an ability [1] [2]. However, the attribute of naturally fallen (shed in the absence of perturbations) melaleuca seeds in terms of their quantity and quality (viability and germinability) prior to biological control implementation in Florida have not been documented. Documentation of the quantity and quality of naturally falling melaleuca seeds before biological control will be essential for comparing with these attributes observed after implementation of melaleuca biological control program. Herein, we sought to document the quantities of seed fall (rain) while assessing their quality (seed germinability percentages) in two habitat types generally occupied by melaleuca trees of various size-categories encountered in southern Florida. We tested the hypothesis that the habitats and tree-size categories will have no effect on the quantity and quality of melaleuca seeds naturally raining from its canopy reservoirs in southern Florida.

2. Materials and Methods

2.1. Study Sites

Three habitat types used in this study were delineated based on hydrological attributes of the sites invaded by melaleuca. These occasionally inundated (N26.049778˚, W80.441556˚ and N26.052444˚, W80.441278˚), and permanently inundated (N26.161667˚, W80.356097˚ and N26.159667˚, W80.365194˚) sites possessing humid subtropical to tropical climate [8] were located in Broward County, Florida (**Figure 1**). The hydrological attributes of these habitats are based primarily on the descriptions of Brown *et al.* 1991) [14] and Kushlan 1991) [15]. Habitats designated as "occasionally inundated" may remain inundated (with less than 0.1 m depth) intermittently for a few hours to several days during or following periods of heavy rain but are neither continuously flooded nor flooded every year, while "permanently inundated" habitats remained inundated year-round [16] where water depth at the research site fluctuated from ca 0.3 - 1.30 m during June of 1997. Soil types in these habitats are dominated by poorly drained organic muck deposited on limestone beds which are generally classified as Histosols [14]. Melaleuca stands are scattered in and around fresh water marshes often associated with the Florida Everglades and the surface water depths in these habitats fluctuate seasonally [15].

2.2. Research Plots and Melaleuca Tree Attributes

Generally, established melaleuca forests form characteristic domes with predominantly larger trees at the center with progressively younger trees, saplings and seedlings near the edges. Two melaleuca domes (hereafter each referred to as a "site") in each habitat were divided into three tree size categories (TSC): "small treesize", at the edge of the dome; "medium treesize", at the mid-section of the

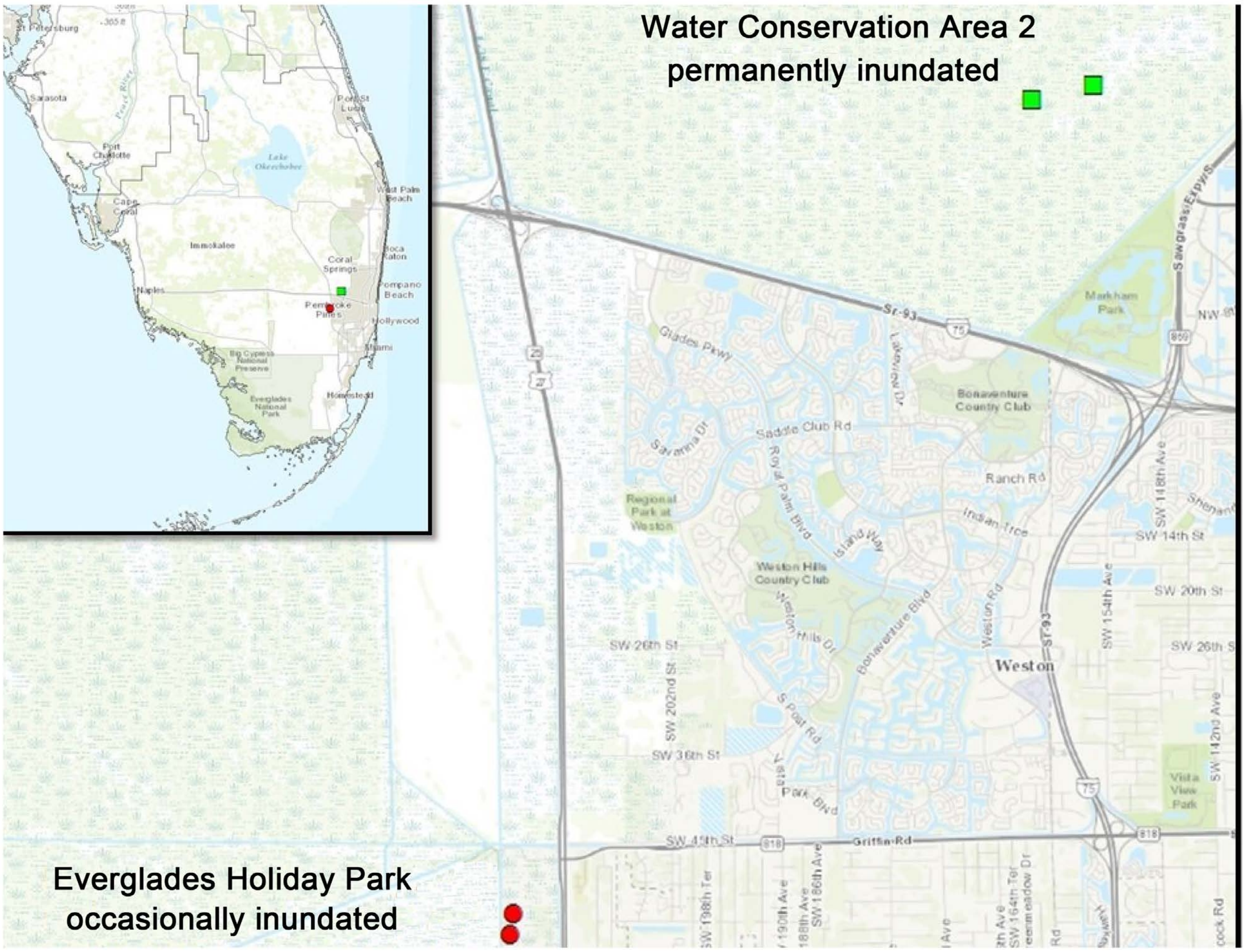


Figure 1. Location of *M. quinquenervia* infested research habitats in Broward County of South Florida, USA where seed fall studies were carried out. Circular (red) and rectangular (green) dots on the map represent the relative locations of the occasionally and permanently inundated habits, respectively.

dome; and "large treesize", at the center of the dome) based upon the prevalent tree diameter at breast height (DBH) measured at 1.3 meter height from the base. The TSCs were delineated based on their existing position in melaleuca stands. Two permanent plots (10 m × 10 m for the large and medium, and 5 m × 5 m for small tree stands) were established in each section of the two sites (each located ca 1 km apart) within each of the two habitats (Figure 1). These plots' dimensions were determined based on the approximate average heights of the majority of tees in the areas (at the onset of the experiment) where the plots were to be located. A total of 24 (3 TSC × 2 plots per TSC × 2 sites × 2 habitats) experimental plots were used in this study.

The DBH of melaleuca trees that were likely to contribute to the seed fall within each habitat and TSC were measured and recorded. These measurements were used to describe the tree attributes (density and DBH; Tables [1] [2]) within each plot in study sites and habitats. Rayachhetry *et al.* (2001) [17] reported 46% - 84% of melaleuca trees to be reproductive as indicated by the presence of the clusters of seed bearing capsules (fruits).

2.3. Seed Fall Trapping

Two wooden framed boxes, each bearing two seed traps, were randomly placed in each plot. Circular seed traps were constructed from 25-cm diameter (0.098 m^2) cylinders that measured ca 15-cm depth and fitted with fine nylon net on one end to catch melaleuca seeds that measured 0.15 - 0.5 mm diameter and 0.6 - 2.0 mm length. One seed-trap was mounted at each of the two corners of two litter trap $plot^{-1}$ using metallic clips, seed traps were emptied at monthly intervals from July 1997-June 1998. For each habitat type, a total of 48 seed traps were monitored during the study (2 sites × 3 tree size categories × 2 plots × 2 boxes × 2 seed traps). Wooden boxes (0.5 × 0.5 m × 16-cm deep) were raised with legs to a height ranging from 20 - 70 cm above ground level in occasionally inundated sites. Water levels in permanently flooded sites fluctuated from 0.3 to 1.3 m. Therefore, the wooden litter trap boxes were modified to float at least 10 cm above the water surface by mounting a capped 3.8-liter plastic jar under each of the four corners of the supporting frame and tying them loosely to a nearby tree to secure them in place [16]. This allowed seed traps mounted on two sides of the wooden boxes to float above the water lavel.

2.4. Seed Quantity

Melaleuca seeds collected from the two seed traps mounted on each box were bulked during collection to maximize seed number for weighing purposes. Therefore, 24 composite (48 seed traps/2) seed samples were collected $habitat^{-1}\cdot month^{-1}$. Each of these composite seed samples were air-dried at room temperature and the foreign objects, such as bark and twig fragments, leaves, insect frass and other dirt particles, were removed. Seeds were either directly counted (if quantities per trap were small) or weighed and sub-sampled, with overall counts extrapolated from the subsamples and the final tallies have been presented as the number of seeds $ha^{-1}\cdot mo^{-1}$.

2.5. Seed Quality

Melaleuca seed quality was measured in terms of viability and germinability percentages based either on 200 seeds or the total number of seeds collected, whichever was greater. The germinability test procedures used in this study were the same as described in Rayachhetry *et al.* (1998). All tests were performed using sterile petri dishes (5-cm diam.), each containing a sterile pad. The pads were soaked with 2 ml of 0.5% 2,3,5-triphenol tetrazolium chloride (TTC) or sterile deionized water (SDW) that left a thin film of liquid on the surfaces. The seeds were spread onto the soaked sterile pads. The dishes were closed and sealed with Parafilm[3] and placed in a dark cabinet drawer at room temperature (25˚C). Seed germinability was assessed on 10 and 14 d after initiation of the testto capture viability and germinability by examining seedmorphology under a dissecting microscope using reflected and/or transmitted light. A seed was considered germinable when an emerging radicle grew out of the seed coat and became visible [10].

2.6. Data Analyses

In this study, the independent variables were habitat types and melaleuca TSCs and the dependent variables were the quantities (number of seeds per unit area of the melaleuca stands) and qualities (seed viability and germinability) of fallen melaleuca seeds. However, another set of confounding variables within habitats are melaleuca tree densities and DBH that may influence quantity and quality of fallen melaleuca seeds in the study sites within habitats. Therefore, prior to determining the effects of habitat and TSCs on seed it was necessary to determine the effects of habitat on these confounding variables in the habitat. The tree density and DHBs of plots within each habitat were pooled and tested for normality using Shapiro-Wilkin's normality test procedures in Sigma Plot [18]. Overall stem density data passed (W-Statistics = 0.936; $P = 0.117$) the normality tests whereas, the DBH data failed (W-Statistics = 0.885; $P = 0.009$) this test. Therefore, double-sided logarithmic transformed (natural log-transformed) data for plot stem density and DBH were analyzed using GLM procedure [19]. Main effects and interaction terms that were not significant ($P > 0.05$) in the model were dropped and the variables with significant ($P \leq 0.05$) terms were included in further ad hoc analyses. Multivariate analysis of variance (MANOVA) was applied to assess habitat and TSC effects on confounding variables (density and DBH) as well as the variables of interest (quantity and quality of fallen melaleuca seeds).

The seed viability and germinability percentages were arc-sine transformed [arcsine value = (sqrt (viability or germinability percentage/100))] to stabilize the variance prior to further analyses to determine the effects of habitat and TSC on the quantity and quality (viability and germinability) of fallen melaleuca seeds. We examined possible correlations between the mean tree density and corresponding quantity of fallen melaleuca seeds within habitat applying Spearman's Correlation Coefficient test procedure on these transformed data. Mean separation for the effects of habitat were performed using Fisher's protected least significant difference (LSD) while the effects of the TSCs were performed using Duncan's Multiple Range Test procedure. Although analyses were performed using double transformed data in all but stem density as indicated above, actual values related to the number of seeds and their viability and germinability have been used in the figures and tables presented herein.

3. Results and Discussion

3.1. Melaleuca Tree Attributes in Study Habitats

The main effects of habitat and TSC on tree (≥1.3 m tall) density were significant while their interaction habitat * TSC was not significant (**Table 1**). Tree DBH in the study sites was not affected by habitat and habitats * TSC but it was affected by TSCs (**Table 1**). Mean density and DBH of the trees in the study sites are presented in **Table 2**. Statistically, stem densities in occasionally inundated habitats were not different across TSC even though there were relatively fewer stems in large tree size categories. On the other hand, stem densities in small and medium TSC in permanently inundated sites were significantly higher than

Table 1. Stem density (# m^2) and DBH (cm) of *M. quinquenervia* among tree size-categories (TSC) within two habitat types of South Florida used in seed fall studies.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Stem Density					
Habitats	1	1.15983945	1.15983945	8.80	0.0078
TSC	2	1.17055204	0.58527602	4.44	0.0262
Habitat*TSC	2	0.12598204	0.06299102	0.48	0.6274
Stem DBH					
Habitats	1	0.01166625	0.01166625	0.59	0.4519
TSC	2	2.97880017	1.48940008	75.32	<.0001
Habitat*TSC	2	0.00398017	0.00199008	0.10	0.9047

Table 2. Tree size-categories (TSC) in the *M. quinquenervia* seed fall studies in two habitats of South Florida.

Tree size-categories	OI[1]		PI[1]	
	Density (trees m^2)	DBH (cm)	Density (trees m^2)	DBH (cm)
Small	1.6667 a[1]	3.7 c	1.9760 a	3.8 c
Medium	1.4900 a	5.4 b	2.8350 a	5.9 b
Large	0.9450 a	8.9 a	1.3900 b	9.3 a

[1]OI = occasionally inundated and PI[1] = permanently inundated. [2]Numbers on the column within habitat followed by different letters are significantly different from each other as per Waller-Duncan's multiple range test at $P \leq 0.05$.

those in large TSC (Table 2). Tree stand attributes, such as tree DBH distribution in a forest stand, are important since this parameter is considered as a good predictor of the canopy-held seed reservoir of the serotinous trees (e.g., [17] [20] [21]). This suggests that the production and releases of melaleuca seeds from trees should increase with an increase in tree DBH. Norghauer and Newbery (2015) [22] studied two tree species, *Microberliniabisulcata* A. Chev and *Tetraberliniabifoliolata* (Harms) Hauman in rain forests of Africa and reported a nonlinear asymptotic increase in seed production and subsequent releases in two masting events. In this case, the examination of correlations between the mean tree densities showed no significant correlation (r = −0.126, P = 0.577, N = 22) with the quantity of fallen melaleuca seeds across two habitats. However, viability (r = −0.363, P = 0.0972, n = 22) and germinability: (r = −0.438, P = 0.0412, n = 22) of fallen melaleuca seeds across two habitats indicated a weak to moderately strong correlation with tree densities. This indicated that melaleuca tree density did not effect seed quantity but had some negative effects on their viability and germinability in the studied habitats.

3.2. Quantities of Fallen Seed by Habitat and TSCs

The main effect of habitat and its interaction with TSC did not have significant influence on the quantity of fallen seeds, whereas the main effect of TSC did (Table 3). Therefore, corresponding seed quantity data from occasionally and

Table 3. The overall effects of habitat and tree-size categories (TSC) on the quantity (number of seeds $m^2 \cdot mo^{-1}$) and quality (viability and germinability) of fallen *M. quinquenervia* seeds in South Florida.

Source	DF	Type III SS	Mean square	F Value	Pr > F
Quantity					
Habitats	1	8.40339422	8.40339422	4.68	0.0312
TSC	2	15.80776453	7.90388226	4.40	0.0129
Habitat*TSC	2	6.99597518	3.49798759	1.95	0.1442
Viability					
Habitats	1	0.36865933	0.36865933	57.23	<.0001
TSC	2	0.08404200	0.0420210	6.52	0.0017
Habitat*TSC	2	0.05019575	0.02509788	3.90	0.0212
Germinability					
Habitats	1	0.34050272	0.34050272	48.22	<.0001
TSC	2	0.08211020	0.04105510	5.81	0.0033
Habitat*TSC	2	0.04083512	0.02041756	2.89	0.0568

permanently inundated habitats were pooled and mean separations were performed by TSCs. The mean number of fallen seeds ($m^2 \cdot mo^{-1}$) and the average number of seeds per tree are presented by TSC (**Table 4**).

The overall quantity (number of seeds $ha^{-1} \cdot mo^{-1}$) of fallen seeds in small and medium TSCs across two habitats were similar but in both these seed quantities were significantly less than the quantities in the large TSCs (**Table 4**). An average of 8947 seeds fell from a single tree in large TSC compared to 3032 and 4513 seeds in medium and small TSCs, respectively (**Table 4**). Woodall (1982) [9] studied seed rain pattern in a mature melaleuca tree stand (4600 trees of >5 cm dbh) and reported seed fall of 2260 seeds $m^2 \cdot wk^{-1}$ or ca 9820 seeds $m^2 \cdot mo^{-1}$, this amount approximately matches to the amount we have for our large TSCs. Rayachhetry *et al.* (2001) [17] conducted a study on melaleuca tree allometry and showed an increase in its canopy-held seed reservoir with the increase in tree sizes. In other systems larger trees in general have also been shown to produce higher number of seeds compared to the trees of smaller sizes (e.g., [23] [24] [25]). These larger trees are expected to generate higher quantities of monthly seed fall in the forest stands. This assumption is corroborated by the results of a study on scots pine (*Pinus sylvestris* L.) that showed an increase in the number of seeds fallen with an increase in tree sizes [26].

3.3. Qualities of Fallen Seed by Habitat and TSCs

The main effects of habitat, TSC, and their interaction terms demonstrated a significant effect on the viability and germinability of fallen melaleuca seeds in our study sites (**Table 3**). Therefore, the seed viability and germinability attributes of fallen melaleuca seeds were analyzed by TSCs within each of the two habitat types.

Table 4. The effects of tree-size categories (TSC) on the quantity (# of seeds) and quality (viability and germinability) of *M. quinquenervia* seeds falling from dehisced canopy-held seed-capsules in two habitats of South Florida.

Tree size-categories	Total seed rain (#s·m^2·mo^{-1})	Sample traps (N)	Average seed rain[1] (#s $tree^{-1}$·mo^{-1})
Small	8221 b[2]	133	4513[1]
Medium	6557 b	131	3032
Large	10446 a	121	8947

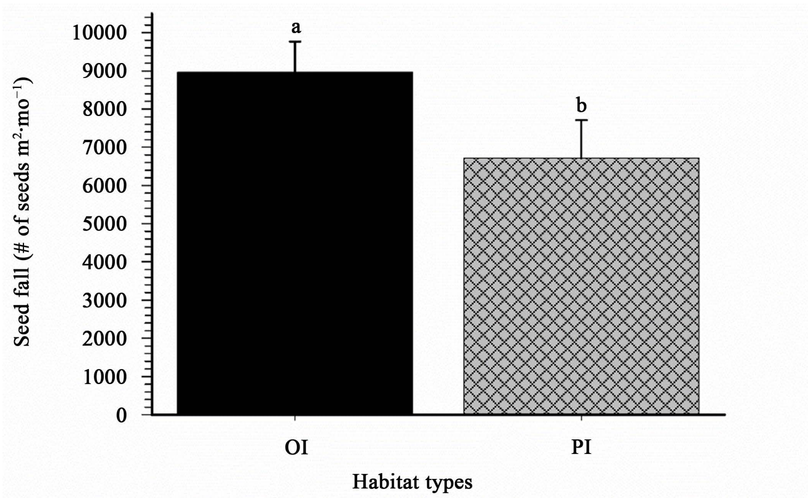
[1]Average number of seeds $tree^{-1}$·mo^{-1} = mean number of fallen seeds m^2·mo^{-1}/average # of trees in OI + PI within corresponding TSCs in Table 2. [2]Numbers on the column followed by different letters are significantly different from each other as per Waller-Duncan's multiple range test at $P \leq 0.05$.

The viability and germinability of fallen melaleuca seeds among TSCs are shown in Table 5. The viability and germinability of fallen seeds between small and medium TSCs in occasionally inundated habitats were significantly different; however, these two attributes of large TSC were not different from those in small and medium TSCs. These results indicated no clear cut TSC effects on the quality of fallen melaleuca seeds in occasionally inundated habitat. On the other hand, the viability and germinability of fallen melaleuca seeds in permanently inundated habitat decreased with an increase in the TSCs. Overall, the viability and germinability of fallen melaleuca seeds had inverse relationship with the TSCs. Previously, melaleuca seeds held in older seed-capsules cohorts have been reported to have low viability and germinability due to their age; on the other hand, the larger trees tend to have older cohorts (crop) of seed-capsules [17]. Consequently, seeds contributed by the older capsule cohorts may have contributed to the lower seed viability and germinability in larger tree TSCs. A similar decrease in seed germinability with an increased age of the cone crop has also been reported in canopy-held seeds of a serotinous tree *Allocasuarina distylla* (Vent.) L. Johnson, and *A. nana* (Seib. ex Spreng.) L. [27].

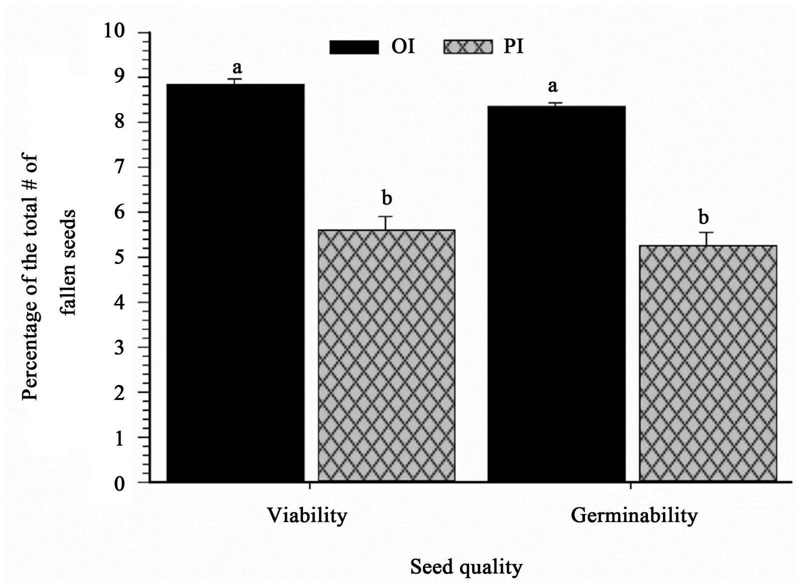
3.4. Summary of Fallen Seed Quantity and Quality

When pooled across TSCs, the quantity (F = 5.94, P = 0.0153), viability (F = 48.55, P < 0.0001), and germinability (F = 42.18, $P \leq 0.0001$) of fallen seeds varied significantly between the two habitats. Overall, the occasionally inundated habitat (8961 seeds m^2·mo^{-1}) had significantly higher seed fall compared to those in permanently (6716 seeds m^2·mo^{-1}) inundated habitat (Figure 2(a)). Also, the viability of fallen melaleuca seeds in occasionally inundated habitat (8.84%) was significantly higher than in permanently inundated habitat (5.47%); the seed germinability in both habitats (8.4% in occasionally inundated and 5.07 in permanently inundated) followed trends similar to those observed in their respective viability (Figure 2(b)). These data indicate that a small fraction of fallen seeds also appeared to remain dormant in both habitats as described by Rayachhetry *et al.* (1998) [10] for canopy-held melaleuca seeds.

When averaged across habitats, the quantity (F = 7.04, P = 0.0010), viability (F = 3.40, P = 0.0346), and germinability (F = 4.65, P = 0.0102) attributes of fallen



(a)



(b)

Figure 2. Summary showing seed quantity (mean number of seeds) and quality (germinability) of *M. quinquenervia* seeds fallen across the three tree size-categories (TSCs) within two hydroperiod based habitat types (OI = occasionally-inundated, PI = permanently inundated)in South Florida; (a) mean seed quantity (number of seeds $m^2 \cdot mo^{-1}$, n = 281 in OI); (b) mean seed quality in terms of the percentage of total number of fallen seeds that were viable and germinable in OI (n = 265) and PI (n = 96). Note, "n" represents the number of seed-traps sampled. Bars with the different letters representing two habitats in a given figure are significantly different at $P = 0.05$ according to Fisher's protected least significant difference (LSD) test.

seeds were significantly different among the three TSCs. Large TSCs (10446 seeds $ha^{-1} \cdot mo^{-1}$) had higher seed fall compared to those in medium (6557 seeds $m^2 \cdot mo^{-1}$) and small (8221 seeds $m^2 \cdot mo^{-1}$) TSCs (Table 4). The viability of fallen melaleuca seeds in small TSC (8.92%) was significantly higher than in medium (7.20%) and large (7.7%) TSCs; the seed germinability in two habitats followed trends similar to those observed in viability (Figure 3).

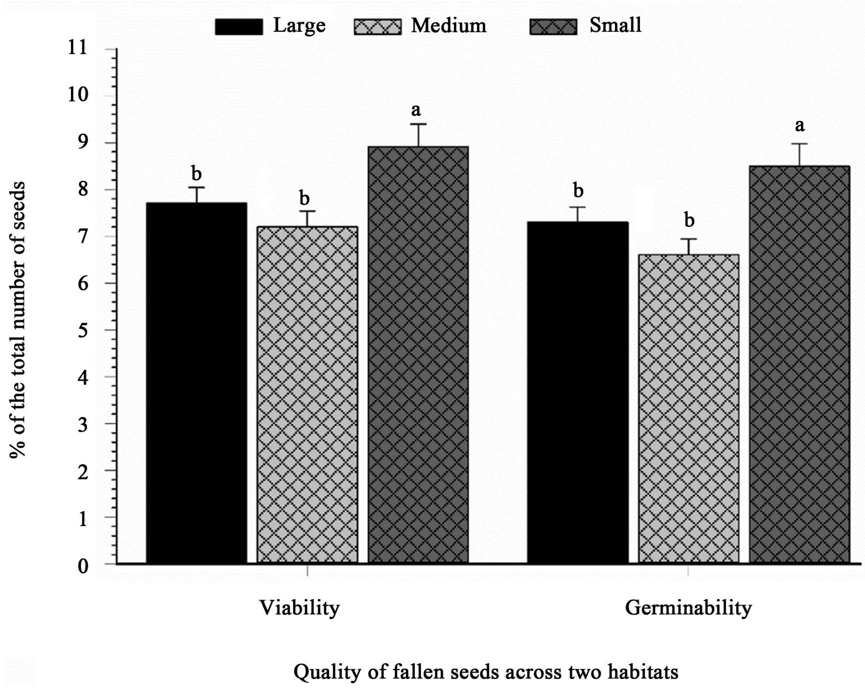


Figure 3. Summary showing the quantity (mean number of seeds) and quality (viability and germinability) of *M. quinquenervia* seeds that fell in three tree size-categories (TSCs) across two (OI and PI) habitats. Mean seed quality expressed in terms of the percentage of total viable and germinable in large (n = 112), medium (n = 125) and small (n = 124) TSCs. Note, "n" represents the number of seed-traps sampled. Bars with the different letters representing seed qualities among three TSCs across two habitats are significantly different at $P = 0.05$ according to Waller Duncan's multiple range tests.

Table 5. The effects of tree-size categories (TSCs) on the quality of *M. quinquenervia* seeds falling from dehisced canopy-held seed-capsules in two habitats of South Florida.

Habitats/Tree-sizes	Viability (% of total)	Germinability (% of total)	Sample traps (N)
OI			
Small	9.8 a	9.3 a	96
Medium	8.0 b	7.4 b	90
Large	8.7 ab	8.3 ab	95
PI			
Small	6.8 a	6.4 a	37
Medium	5.3 a	4.8 ab	41
Large	3.5 b	3.4 b	26

[1]Numbers on the column within habitat followed by different letters are significantly different from each other as per Waller-Duncan's multiple range test at $P \leq 0.05$.

In summary, the quantity and quality of fallen melaleuca seeds was higher in occasionally inundated than in permanently inundated habitats (Table 4 and Table 5) and Figure 2(a) and Figure 2(b)). This trend is consistent with Rayachhetry *et al.* (1998) [10] who reported less germinability (6.0%) of canopy-held seeds from permanently inundated sites as compared to 7.8% from those in dry (occasionally-inundated) habitats, since canopy-held melaleuca seed reservoirs contribute to the seed fall in the respective studied habitats. On the other hand, melaleuca stands with predominantly smaller TSCs in both habitats had higher viability and germinability of fallen melaleuca seeds. One explanation for higher quality of seeds among the smaller TSCs may be related to their relative location along the periphery of the stand where their flowers were more accessible to pollinators than those of older trees located within the interior. This hypothesis requires further testing but pollens and pollinators have been reported to play important roles in seed qualities among flowering plants and increased pollinator populations often result in better seed set and greater seed quality in flowering plants [24].

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