Int. J. Plant Sci. 159(4):648–654. 1998.
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1058-5893/98/5904-0014$03.00

REGENERATION POTENTIAL OF THE CANOPY-HELD SEEDS OF *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA

Min B. Rayachhetry,[1,*] Thai K. Van,† and Ted D. Center†

*Fort Lauderdale Research and Education Center, University of Florida, 3205 College Avenue, Fort Lauderdale, Florida 33314, U.S.A.; and †USDA-ARS, Aquatic Weed Research Laboratory, 3205 College Avenue, Fort Lauderdale, Florida 33314, U.S.A.

Melaleuca quinquenervia produces and maintains extensive seed reservoirs in the forest canopy. We collected capsules from different infructescences (clusters; Cluster I is the youngest, located at the most distal position, and Cluster VII is the oldest, located at the most proximal position) on branches from dry, seasonally flooded, and permanently flooded habitats. Extracted seeds were soaked for 10 d in sterile deionized water and/or 2,3,5,-triphenol tetrazolium chloride (TTC) stain to assess viability. Microscopic inspections revealed that only 15% of the seeds were embryonic (filled), 50% of embryonic seeds were viable (stained red with TTC), and 73% of viable seeds were germinable after 10 d. The remaining 27% of viable seeds may have been dormant or, possibly, required special conditions for germination. A higher percentage of seeds were embryonic on trees at permanently flooded habitats (18%) when compared to dry (14%) or seasonally flooded (14%) habitats. Overall seed viabilities and germinabilities were comparable among the three habitat types. Proportions of filled seeds were constant among infructescence positions within each habitat. Both viability and germinability of seeds varied with infructescence age, both being highest in Clusters II–V and lowest in Cluster VII.

Introduction

Melaleuca quinquenervia (Cav.) Blake (paperbark or broad-leaved paperbark) is an aggressive weed tree of Australian origin that has invaded sensitive Everglades ecosystems and surrounding areas in south Florida. Introduced in the early 1900s (Meskimen 1962), paperbark currently infests 197,846 ha.[2] Within recent years, rapidly expanding paperbark populations have invaded disturbed as well as undisturbed habitats. This has displaced native flora, reduced wildlife habitat, increased fire hazards, and exacerbated human health problems (Morton 1962; Hofstetter 1991). The invasive nature of this species may be attributable to its prolific seed-producing ability, broad ecological amplitude, and a general lack of natural enemies coupled with favorable characteristics of the south Florida environment (Hofstetter 1991; Turner et al., in press).

Vardaman (1994) studied paperbark pollination, fertilization, and seed development and found it to be self-compatible and autogamous, but it also promotes outcrossing. According to Meskimen (1962), some paperbark trees become reproductive within a year of germination, and flowering events occur several times a year. A flower spike reportedly can produce 30 to 70 sessile capsules with each containing 200 to 350 seeds and these capsules can remain attached to the trunks, branches, or twigs for over 7 yr (Meskimen 1962). These open and release seeds after their vascular connections are disrupted by increased bark thickness or stresses such as fire, frost, mechanical damage, herbicide treatments or self-pruning of branches (Woodall 1982; Hofstetter 1991).

Simpson et al. (1989) distinguished between aboveground (canopy) and soil seed banks for tree species in different communities. The aboveground seed bank of paperbark consists of seeds held in capsules on branches in the canopy. While massive, synchronous seed release occurs in response to various stresses, some capsules open successively in a nonsynchronous manner, resulting in a light but constant seed rain (Woodall 1982; Hofstetter 1991). Viability, germinability, and longevity of canopy-stored seeds have not been compared among sites or habitats in either south Florida or Australia, yet paperbark seed production and germinability are thought to be site (habitat) specific (Browder and Schroeder 1981). Meskimen (1962) showed 3%–28% germination of air-dried paperbark seeds stored for 10 wk. Woodall (1982) reported decreased germinability associated with decreased seed weight. Myers (1975) described optimal environmental conditions for seed germination as alternating 12-hr wet and dry cycles or continuously wet conditions at 23° to 26°C. However, viability and germinability of seeds stored within aboveground reservoirs have not been studied.

Control of seedlings may be accomplished by intentional flooding, controlled burning or foliar spray of herbicides (Timmer and Teague 1991; Bodle et al. 1994). To plan site-suitable control strategies, resource managers need to understand seedling recruitment based on viability and germinability of canopy-stored seeds. Such information will also aid postrelease assessments of newly introduced biological control agents (Turner et al., in press) that directly or indirectly reduce the quantity of canopy-stored seeds. Therefore, the purpose of this study was to investigate the viability and germinability of canopy-stored seeds from paperbark trees growing in habitats with differing hydroperiods in south Florida.

[1]Author for correspondence and reprints.

[2]A. P. Ferriter, personal communication, 1994. South Florida Water Management District, 3301 Gun Club Road, West Palm Beach, Florida 33416, U.S.A.

Manuscript received February 1997; revised manuscript received March 1998.

Material and Methods

Habitats

Three types of habitats (dry, seasonally flooded, and permanently flooded) in Broward, Collier, Dade, and Palm Beach counties were identified for seed-capsule collection. Dry habitats included upland areas like roadsides, golf courses, and urban settings. These sites consisted of well-drained ground that consistently lacked standing water. Low-lying areas with no standing water during spring or early summer or sites with standing water all year round were considered seasonally flooded and permanently flooded habitats, respectively. At least two sites were sampled from each habitat type.

Sample Collection

A total of 17, 6, and 7 trees were sampled from dry, seasonally flooded, and permanently flooded habitats. Sample trees over 5 m tall were deliberately chosen either from the edge of a mature stand or from an isolated place to obtain the maximal number of infructescence or capsule-cluster positions (age cohorts by inference, henceforth referred to as clusters). A branch bearing the greatest number of clusters was harvested. Clusters located more proximally on a branch are relatively older than more distal ones due to auxotelic growth (Briggs and Johnson 1979). Adjacent clusters located on the same stem axis were considered distinct if they were separated by a series of leaves and/or leaf scars. The series was followed proximally along a given branch sample until no older clusters were observed. The clusters were designated as Cluster I to VII accordingly, with Cluster I being the youngest (occupying the most distal position) and the Cluster VII the oldest (the most proximal position). The flowering history of the branches was unknown, so precise ages of cluster positions could not be determined; but we assume that capsules located at the same cluster positions within a habitat type were of similar age. Comparisons among cluster positions were therefore made only within habitat types.

Seed Extraction

All capsules from an individual cluster position were placed in an open plastic bag and air-dried under greenhouse conditions at 25°–40°C. Seeds from young capsules were usually forcibly released by mechanical disruption of the capsule wall, but older capsules dehisced and released seeds within 2–3 d. Seed samples from individual clusters were separated from capsules, placed in plastic bags, sealed, and stored at room temperature (25°C) for 7–15 d.

Seed Fill, Viability, and Germinability

Whole (uncut) seeds were used in seed fill, viability, and germinability studies. All tests were performed using sterile petri dishes (5-cm diam; Microfiltration Systems, Dublin, Calif.), each containing a sterile pad. The pads were soaked with 2 mL of 0.5% 2,3,5,-triphenol tetrazolium chloride (TTC; Sigma Chemical Co., St. Louis) or sterile deionized water (SDW) to leave a glistening film of liquid on the surfaces. Seeds with living, respiring embryos stained red after treatment with TTC (Grabe 1970). These seeds with red-stained embryos were considered viable. A seed was considered germinable if the emerging radicle was visible and grew out of the seed coat (Berrie 1984). A preliminary test gave comparable germination percentages for TTC and SDW. However, further seedling growth was inhibited by TTC treatment. Both techniques provided comparable rates of radicle emergence and the emergence percentage did not change after a 10-d experimental period.

Two samples, each containing two hundred seeds were randomly withdrawn from a lot of several thousand seeds for each cluster cohort for both the germinability and viability tests. These were evenly spread onto the soaked sterile pads. The dishes were closed and sealed with Parafilm and placed in a dark cabinet drawer at room temperature (25°C). After 10 d, the seeds were evaluated for fill, viability, and germinability by examining their condition under a dissecting microscope using reflected and/or transmitted light. Filled (embryonic) seeds in both SDW and TTC treatments appeared black (nontransparent) when viewed with back lighting. The TTC-treated seeds were categorized into non-stained (glassy white), lightly pink, or cherry red. Nonfilled seeds (hereafter referred to as empty seeds) appeared translucent (TTC or SDW treated) when back-lit. Presence or absence of embryos, and color development in SDW- or TTC-treated filled or empty seeds was verified by rupturing the seed coats. Seeds containing cherry-red embryos were classified as viable while seeds containing lightly pink or glassy-white contents were nonviable or nongerminable (Grabe 1970).

Data Analyses

Data were analyzed using GLM procedures (SAS 1985). Arc-sine transformed percentages of seed fill, viability, and germinability values were analyzed using one-way analysis of variance with habitat as an independent variable. Capsule cluster positions were considered independent variables and the arc-sine transformed data were analyzed using one-way analysis of variance. Mean separations were performed using Fisher's protected least significant difference (LSD).

Photographs

Representative photographs of SDW- or TTC-treated seeds or resulting seedlings were taken through a dissecting microscope using epi- and/or back-light illumination.

Results

Capsule Cluster Position

Figure 1*A* shows a portion of a branch bearing numerous serotinous woody capsules in a series of cluster positions. Usually, consecutive clusters are separated by vegetative growth. This is evidenced by a series of leaves or leaf-scars between clusters (fig. 1*A*); however, one cluster sometimes immediately succeeds another. In these cases, it is difficult to distinguish cluster positions. For example, up to five successive clusters accounting for a total of 30 cm length were observed which were intervened by inconspicuous bud-scale scars. However, the cluster positions shown in figure 1*A* or those used in seed fill, viability and germinability studies were distinctly separated by a series of leaves or leaf-scars, but had no bud-scale scars or capsule-size differences within a cluster position. This insured that capsules forming a given cluster position were of equal age for a given tree.

General Seed Characteristics

The mean length and the diameter at broadest part (end that attaches to placenta) of seed were 1.20 mm

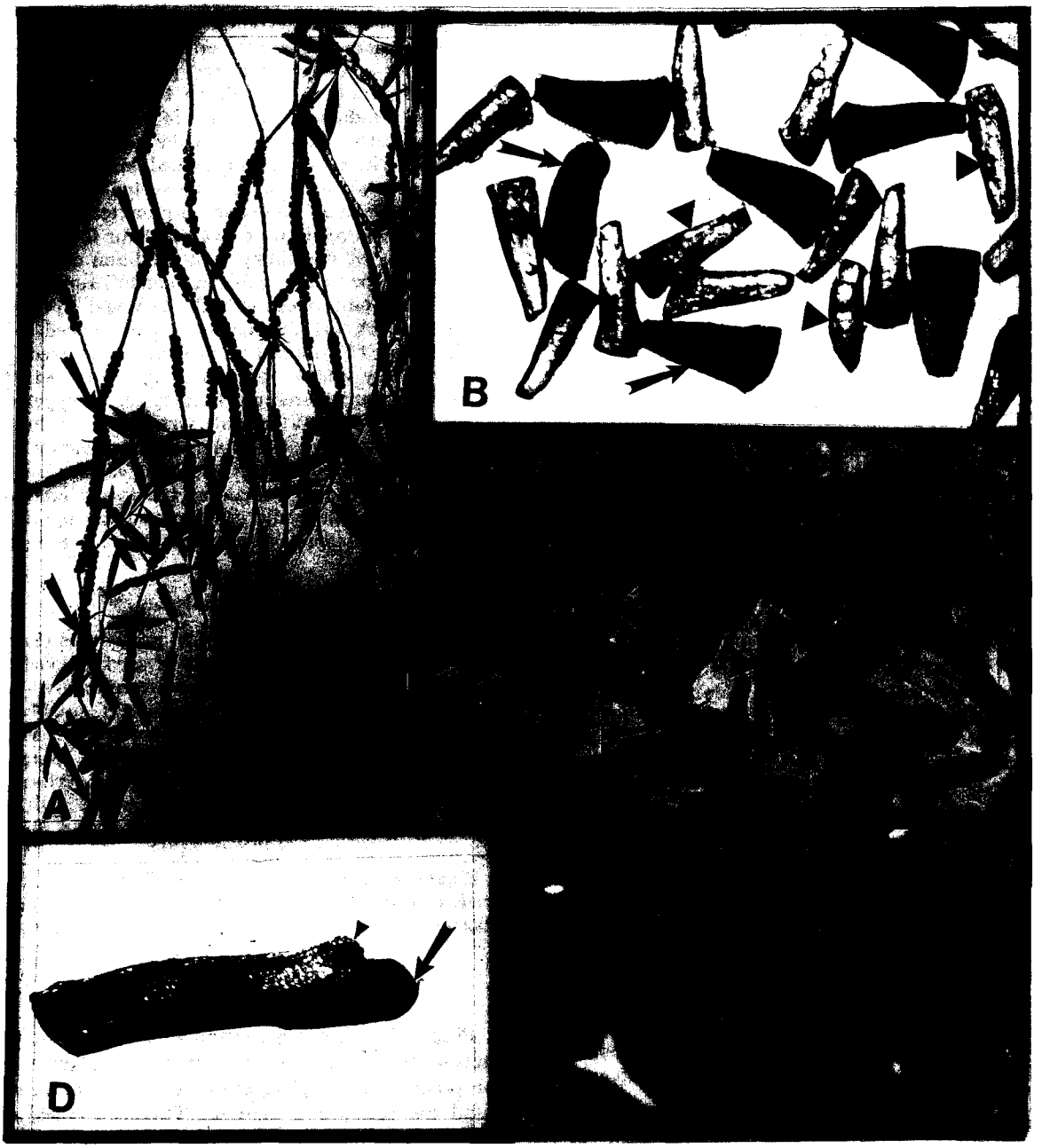

Fig. 1 Paperbark infructescence or capsule-cluster (3–7 cm long) positions, seed viability, and germinability. *A,* A branch showing capsule clusters positions; note capsule clusters (arrows) separated by a gap (leaf scars), the youngest clusters occur adjacent to branch apex and the oldest toward branch base. *B,* Seeds soaked 12 h in sterile deionized water illustrating filled (arrows) and empty (thick triangles). *C,* Seeds soaked in 0.5% 2,3,5-triphenol tetrazolium chloride for 10 d; note filled seeds that were stained cherry red (arrows), stained and germinated (thin triangles), and empty (thick triangles). *D,* A triphenol tetrazolium chloride–treated germinating seed; note a radicle (arrow) emerging from a seed coat (thin triangle). *E,* A seedling at cotyledonary stage in sterile deionized water treatment.

(range 0.60 to 2.00 mm) and 0.26 mm (range 0.15 to 0.05 mm), respectively. Filled and empty seeds were easily distinguished. Filled seeds soaked in SDW appeared dark-brown when back-lit (fig. 1*B*). Seed coats of filled seeds were soft and contained soft tissues inside. Empty seeds appeared translucent (fig. 1*B, C*) and their seed coats were brittle and hollow. The filled seeds were relatively cylindrical. Some of them remained unstained (glassy white) while others stained either cherry-red or light pink with TTC (fig. 1*C*). The unstained and light pink embryos did not show a growth response to soaking in SDW or TTC as evidenced by the relatively smaller cotyledons and radicles when compared with the cherry-red-stained embryos. Seeds containing cherry-red-stained embryos showed an epigeal germination evidenced by radicle emergence (fig. 1*D*) followed by hypocotyl elongation and seed coat shedding. Radicle emergence of most

Table 1 Effects of Habitat on Fill, Viability, and Germinability of Paperbark Seeds

Variable	Means (%)			
	Overall	Dry	Seasonally flooded	Permanently flooded
Filled of total	14.9 (±0.7)	14.0 (0.9)b	13.9 (±1.4)b	17.7 (±1.7)a
Viability of total	8.9 (±0.5)	9.1 (±0.7)a	9.7 (±1.3)a	7.6 (±0.6)a
Germinability of total	7.2 (±0.5)	7.8 (±0.7)a	7.1 (±1.2)a	6.0 (±0.7)a
Viability of filled	61.8 (±2.1)	61.7 (±2.6)a	66.3 (±5.0)a	58.4 (±4.6)a
Germinability of filled	50.1 (±2.3)	51.2 (±2.8)a	52.9 (±5.8)a	45.1 (±4.9)a
Germinability of viable	72.8 (±2.2)	76.9 (±2.7)a	66.7 (±6.2)a	68.1 (±4.4)a

Note. Means (standard error) among dry, seasonally flooded, and permanently flooded habitats within a row with the same letter(s) are not significantly different from each other at $P = 0.05$, according to Fisher's protected least significance difference (LSD).

germinable seeds soaked in either SDW or TTC occurred within 10 d. Seedling growth and development in TTC treatments ceased after seed coat shedding (fig. 1*C*); in contrast, seedlings originating from SDW treated seeds continued to grow and develop beyond this stage (fig. 1*E*). Nonetheless, the germinability, i.e., radicle emergence from the seed coat, was not affected by TTC.

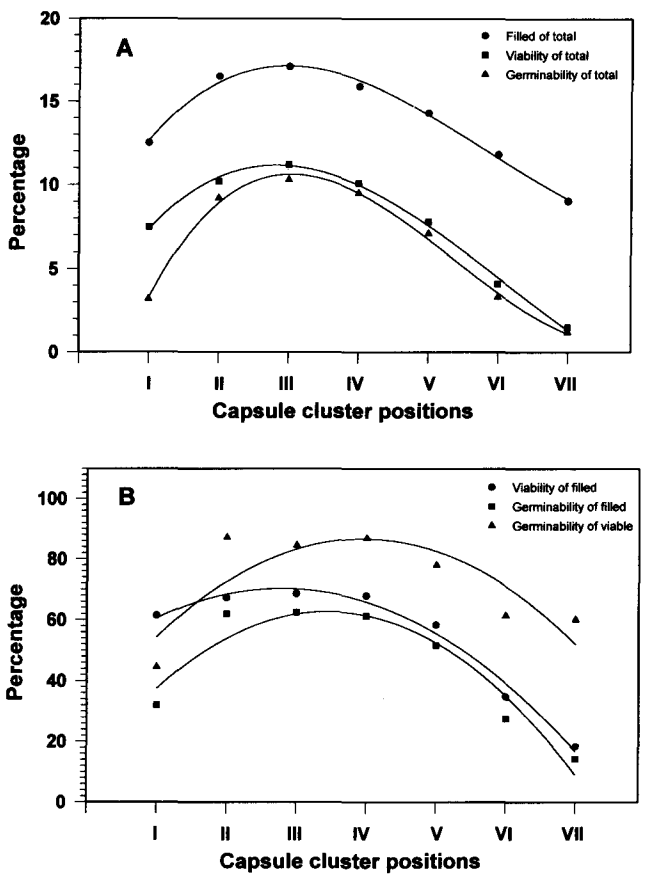

Fig. 2 *A*, Overall effects of capsule-cluster positions (CC) (ranked as younger to older cluster) on percentage of fill (F), viability (V), and germinability (G) of paperbark seeds across three habitats. $F = 5.93 + 8.54CC - 1.93CC^2 + 0.11CC^3$ ($r^2 = 0.99$), $V = 1.30 + 7.78CC - 1.79CC^2 + 0.10CC^3$ ($r^2 = 0.99$), and $G = -7.59 + 13.83CC - 3.18CC^2 + 0.20CC^3$ ($r^2 = 0.99$). *B*, Overall effects of the age (ranked as younger to older cluster) of capsule clusters (CC) on the viability of filled (VOF) germinability of filled (GOF) and germinability of viable (GOV) paperbark seeds across three habitats. $VOF = 46.80 + 16.80CC - 3.01CC^2$ ($r^2 = 0.98$), $GOF = 12.56 + 29.14CC - 2.24CC^2$ ($r^2 = 0.92$), and $GOV = 28.70 + 29.35CC - 3.724CC^2$ ($r^2 = 0.70$).

Overall Seed Fill, Viability, and Germinability

It makes little sense to base viability percentages on empty seeds, or germinability percentages on nonviable seeds, so the most important biological attributes are the percentage of the total seeds that are filled, the percentage of the filled seeds that are viable, and the percentage of the viable seeds that are germinable. However, other authors have not recognized empty or nonviable seeds and presented "viability" estimates as the percentage of the total paperbark seed crop that germinated. Therefore, in addition to the above mentioned attributes, we present our data in terms of these parameters as well to enable comparisons with previously published information (Meskimen 1962; Myers 1975; Woodall 1982).

Overall, an average of 15% (1%–55%), 9% (0%–41%), and 7% (0%–41%) of the total seeds were filled (embryonic), viable (based on TTC-test), and germinable (within 10-d of soaking), respectively (table 1). Thus, over 85% of canopy-stored seeds were empty. Viability and germinability of filled seeds averaged 62% (0%–98%) and 50% (0%–98%), respectively, and 73% (0%–100%) of viable seeds germinated after 10 d.

Habitat type had a significant effect on the proportion of the total seed crop with filled seeds, but had no effects on the viability and germinability percentages of filled seeds (table 1). Trees in permanently flooded habitats held a somewhat higher proportion of filled seeds (18%) than dry and seasonally flooded habitats (both 14%). Viability and germinability of the total, viability and germinability of the filled, and germinability of the viable seed crop were not affected by habitat types. Similarly, the proportions of the viable germinable seeds were similar among the three habitats.

Position (i.e., age by inference) of capsule clusters influenced seed fill, viability, and germinability percentages (fig. 2*A*, *B*). Overall percentages of total seeds with respect to all three parameters followed similar trends (fig. 2*A*). As shown in figure 2*A*, fill, viability, and germinability percentages increased from Clusters I to II, became maximal at Clusters II through

Table 2 Effects of Capsule-Cluster Positions (Ranked as Younger to Older Cluster) on Fill, Viability, and Germinability of Paperbark Seeds within a Habitat Type

Dependent variable	Capsule cluster/mean (%)						
	I	II	III	IV	V	VI	VII
Dry habitat:							
Filled of total	12.4 a	14.4 a	15.8 a	18.1 a	13.3 a	11.8 a	9.0 a
Viability of filled	68.9 ab	76.5 a	65.7 ab	67.1 ab	52.4 bc	34.7 cd	18.3 d
Germinability of viable	63.9 b	91.1 a	85.4 a	86.2 a	70.9 ab	61.4 b	60.0 b
Seasonally flooded habitat:							
Filled of total	13.6 a	14.2 a	17.1 a	5.3 a	6.3 a	...*	...
Viability of filled	49.2 b	62.7 b	88.9 ab	100.0 a	83.0 ab	...	...
Germinability of viable	20.4 b	91.1 a	89.1 a	100.0 a	96.2 a	...	...
Permanently flooded habitat:							
Filled of total	11.6 b	23.6 a	19.7 ab	14.5 ab	18.9 ab	...	...
Viability of filled	60.3 a	52.8 a	57.8 a	62.5 a	61.9 a	...	...
Germinability of viable	31.9 b	73.8 a	79.1 a	85.1 a	85.7 a	...	...

Note. Means (%) within a row with the same letter(s) are not significantly different from each other at $P = 0.05$, according to Fisher's protected least significance difference (LSD).

*These capsule clusters were not found on sampled trees.

IV, then progressively decreased at more proximally located clusters.

Filled-seed viability was low in Cluster I, relatively constant among Clusters II through IV, but gradually decreased at more proximal positions (fig. 2*B*). Viability of filled seeds was greatest at Cluster III (68%) and least at Cluster VII (18%). Germinability percentages of filled seeds increased from 32% at Cluster I to 62% at Cluster II and remained relatively unchanged to Cluster IV; however, it gradually decreased to 14% by Cluster VII. Germinability percentages of viable seeds followed a trend similar to that for filled seeds. At Cluster I, only 44% of the viable seeds germinated compared to 87% at Cluster II. These percentages remained relatively unchanged in Clusters II through V, then decreased to about 60% in Clusters VI and VII.

Seed Fill, Viability, and Germinability by Habitats

Dry

Some of the sampled trees in dry habitats had up to seven distinct cluster positions on a given branch, but the majority had two to five. Percentages of total filled seeds were not significantly different across these cluster positions (table 2). Viability of filled seeds was similar in Cluster I through IV and it gradually decreased from Cluster V to VII. Germinability of viable seeds was significantly low in Cluster I, VI, and VII compared to the Cluster II through V.

Seasonally Flooded

Some of the sampled trees in seasonally flooded habitats had up to five cluster positions. A majority of the trees had Cluster I through III. The percentage of total seed-fill was relatively constant among cluster positions (table 2). The percentage of filled seeds that was viable or the percentage of viable seeds that was germinable increased with the cluster age and attained 100% by Cluster IV, then decreased slightly at the Cluster V.

Permanently Flooded

The number of cluster positions on branches of sampled trees in permanently flooded habitats were comparable to those in seasonally flooded habitats. The percentages of total seed-fill were relatively higher in Cluster II, III, and V than in Cluster I and IV (table 2). In general, the viability of filled seeds remained unaffected throughout the cluster positions. The germinability percentage for viable seeds tended to be lowest in the Cluster I (youngest capsules) but otherwise seemed unaffected by cluster positions.

Discussion

A moderate serotiny appears to be prevalent in paperbark. This attribute in other plants is considered a mechanical defense against seed predation and an adaptation to fire (le Maitre and Midgley 1992; Enright et al. 1996). In paperbark, the accumulation of seed-filled capsules in the canopy (Meskimen 1962; Hofstetter 1991) comprises extensive aboveground seed reservoirs. Occurrence of five successive clusters separated by inconspicuous bud-scale scars confirmed previous reports that indicate paperbark's ability to flower up to five times a year (Meskimen 1962; Hofstetter 1991). These were probably produced within a year due to successive flowering episodes with a little intervening vegetative growth on the indeterminate axis. Such an attribute contributes enormously to the pool of canopy-stored paperbark seeds.

Filled and nonfilled paperbark seeds that we distinguished during microscopic examinations are probably equivalent to Woodall's (1982) fertile and infertile seeds, respectively. Similarly, heavier seeds separated by his wind-tunnel technique were probably the filled portion of the seed crop. The filled paperbark seeds staining cherry-red with TTC, are comparable to Gra-

be's (1970) description for viable and germinable seeds. Hydrogen ions produced by respiring cells combines with TTC and gives red pigmentation to healthy living tissues, pale or mottled pigmentation to aged tissue, and no pigmentation to dead tissues (Colbry et al. 1961). Radicle extension in a majority of these cherry-red stained paperbark seeds occurred within 10 d indicating that these seeds are germinable.

Mode of seed development in paperbark is not known. Endosperm in the mature seeds in Myrtaceae is reported to be scanty, starchy or absent (Zomlefer 1994). Seeds in some plants mobilize their reserves from nonliving endosperm and store as reserve food in cotyledons and the mature seeds may become scantily endospermic or nonendospermic (Salisbury and Ross 1969; Berrie 1984). Some of the filled seeds in Cluster I (youngest capsule crop) of paperbark remained glassy white in TTC, indicating the presence of predominant endosperms associated with immature embryos. Myers (1975) suggested that the paperbark seeds require a ripening period within the capsules. In our study, some capsules in Cluster I had to be forcibly opened, while seeds from Cluster II and beyond readily opened and liberated seeds upon drying. Some of the seeds forcibly liberated may have been filled with well developed endosperm but contained immature embryos. These embryos may have died after the capsules were detached from the branch for processing for this study, and thus failed to stain. Alternatively, the reduced respiration activities associated with undifferentiated embryonic tissue may have been inadequate to be picked up by TTC test. Capsules at Cluster II to V showed highest percentages of seed viability and germinability. However, these two parameters decreased significantly at Cluster VII. Meskimen (1962) reported a similar germination trend for cluster positions on a branch of paperbark tree from the west coast of south Florida. A decrease in seed viability and germinability with crop age has also been reported for canopy-held seeds of *Allocasuarina distyla* (Vent.) L. Johnson and *A. nana* (Sieb.ex Spreng.) L. (Pannell and Myerscough 1993). Such a reduction in viability and germinability of seeds in older capsule crops may be attributed to the normal embryonic aging process. Unstained, glassy-white or pale mottled content in seeds from older crops appeared to represent seeds that had no viability whereas lightly pink-stained embryos seemed associated with the low seed vigor. This latter condition is either indicative of immature seeds in youngest capsules or an early sign of seed deterioration in relatively older infructescences.

Some of the paperbark seeds that developed cherry-red stain did not germinate, possibly evincing some kind of dormancy. These dormant seeds may contribute to a transitory soil seed bank. This assumption is supported by Wade (1981), who reported that the seeds buried in superficial soil horizons remain viable for more than 10 mo. Fire adaptation (Hofstetter 1991) in concert with transitory soil seed banks suggests that paperbark exhibits moderate serotiny compared with other more highly fire-adapted species. *Banksia hookeriana* Meissn., for example, lacks soil seed banks and show higher degrees of serotiny (Enright et al. 1996).

Reasons for the occurrence of a small percentage (15%) of embryonic seeds in canopy-stored capsules of paperbark are not known. A very low percentage of seed set (1%–2% of total ovules in an ovary) has been reported for other *Melaleuca* species in Australia (Barlow and Forrester 1984). Barlow and Forrester (1984) suggested that low pollen fertility, gametophytic self-incompatibility, stigma clogging, and other prezygotic mechanisms may account for the low seed set in the *Melaleuca* species they studied. Some mechanisms that cause low seed-set in other flowering plants have been listed by Arathi et al. (1996). Occurrence of low seed set or seed fill in many dicotyledonous plants has been attributed to various causes such as (1) an adaptive strategy of plants to discourage seed predation (Coetzee and Giliomee 1987); (2) lack of adequate pollens or pollinators or competition among fertilized zygotes (Uma Shaanker et al. 1988; Bawa et al. 1989); (3) the absence of fertilization, death of the embryo during early embryogenesis, or weevil damage (Shevchenko 1994); (4) seed tree age and dry summers causing reduced shoot length and premature senescence of embryos (Klein and Roloff 1993); or (5) density of flowering plants that affect pollinator behavior, which in turn, may effect pollination success (Schmitt et al. 1987; Allison 1990). The ratio of fertile to nonfertile seeds in South African Proteaceae decreases slightly with increased insect granivory (Mustart et al. 1995). One or more of these factors may cause low seed-fill, reduced viability of filled seeds, and decreased germinability of viable seeds in paperbark.

Despite statistical significance, the differences in seed-fill, viability, and germinability percentages among habitats were slight and therefore may not be biologically significant. However, the results show that only a small proportion of canopy-stored seeds are regenerative and viability and germinability of seeds decrease significantly with capsule age; therefore, the canopy-stored seeds in older capsules may not contribute as much to natural regeneration as those in mid-aged capsules. Biological control agents that reduce overall flower/fruit production and interfere with healthy embryogenesis through defoliation or impairment of physiological processes of trees may reduce the seed quality and quantity and hence invasive potential of paperbark in south Florida.

Hofstetter (1991) estimated that a 10-m-tall open-grown tree may bear 20 million or more canopy-stored seeds. In a recent survey, we estimated that a paperbark tree with 38 cm dbh and 21 m height in a dry habitat of south Florida may bear as much as 34.2 kg of fresh (8.7 kg dry) capsules containing 1.7 kg (about 51 million) of dry seeds (unpublished data). This tree may bear about 5.6 million (9% of 51 million) viable seeds that are capable of producing seedlings. Overall, our findings show a large proportion (85%) of canopy-

stored paperbark seeds to be empty (nonembryonic). However, the small proportion of viable and germinable seeds still represent an immense seed crop and their sustained release confers a competitive advantage over native plants. Further elucidation of the underlying factors (population genetics, mechanism of flower induction and seed development, and associated pests and pathogens) affecting seed-set in the native and adventive ranges of paperbark may help to develop more effective control strategies and aid in the selection of appropriate biological control agents as suggested by Turner et al. (in press).

Acknowledgments

We thank Mr. Jack Kramer and Mr. Keith Moskowitz for field and laboratory assistance and Drs. R. Pemberton and F. W. Howard for reviewing the manuscript.

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