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Biological Attributes of The Canopy-held Melaleuca Seeds in Australia and Florida, U.S.[1]

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The paperbark tree *Melaleuca quinquenervia* (Cav.) S.T. Blake (melaleuca) is invasive in southern Florida, U.S., but benign in its native range (eastern Queensland and northeastern New South Wales, Australia). As part of an ongoing study to explain this dual nature, we compared the biological attributes of canopy-held seeds between the two countries by collecting infructescences (capsule clusters) from branches of open-grown trees in dry to seasonally flooded habitats and comparing branch-position cohorts in terms of capsule densities and seed quality. The infructescence lengths were similar in both countries, but gaps (scars from aborted capsules) within infructescence axes were more common on trees in Australia than on trees in the U.S. This difference was associated with high incidences of flower or fruit abortion in Australia. Consequently, capsule density on infructescence axes was three per cm in Australia compared to eight per cm in the U.S. This resulted in 18 and 49 capsules per infructescence in Australia and the U.S., respectively. Each infructescence in Australia contained ca. 5,000 seeds with <200 viable, compared to ca. 13,000 seeds in the U.S. with >1,200 viable. Seed quality also differed with 9% vs. 14% of seeds containing embryos, 39% vs. 63% of embryonic seeds being viable, and 34% vs. 52% of viable seeds being germinable in Australia and Florida, respectively. The proportional viability and germinability of embryonic seeds did not vary consistently among infructescence-position cohorts in Australia, whereas in the U.S., the proportions were greatest in middle-aged and least in youngest and oldest infructescences. Overall quality and quantity of canopy-held seeds were reduced in Australia when compared to the U.S.

Key words: Fruit set, invasive tree, *Melaleuca quinquenervia*, paperbark tree, seed biology, seed germination, seed viability.

INTRODUCTION

Biological attributes of invading plant species include high reproductive capacity, superior competitive ability, morphological or physiological plasticity, and rapid growth (Browder and Schroeder 1981, Roblin 1994, Rejmanek and Richardson 1996, Goodwin et al. 1999). The Australian tree, *Melaleuca quinquenervia* (family: Myrtaceae), also known as broad-leaved paperbark or melaleuca, exhibits many of these invasive traits in its adventive range in southern Florida, U.S. (Meskimen 1962, Woodall 1982, Hofstetter 1991, Rayachhetry et al. 1998). Unfortunately, little is known about the biology of this species in Australia, so existing knowledge, based largely on data from the U.S., lacks an evolutionary context.

Melaleuca trees are self-compatible and autogamous, but also are capable of outcrossing (Vardaman 1994). Some saplings may become reproductive within a year after germination, and multiple flowering events may occur on a given stem in a single year (Meskimen 1962). Each flower spike produces an infructescence of 30 to 70 serotinous capsules, with each capsule containing up to 350 seeds (Meskimen 1962). The capsules persist on the stems for several years (Meskimen 1962, Van et al. 2002) and open to release seeds only when they dessicate (Woodall 1982, Hofstetter 1991). Thus, a 21-m tall open-grown tree bears 34 kg of mature capsules containing ca. 100 million seeds with the potential to produce as many as 9 million seedlings (T. K. Van, pers. obs.). Furthermore, having evolved in Australia, melaleuca is preeminently fire-adapted, with massive seed release occurring after exposure to the wildfires (Turner et al. 1998) typical of the Everglades region.

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While massive, synchronous seed release occurs only in response to fire, drought, and herbicide damage, a portion of the capsules also open successively, in a non-synchronous manner, producing a light but constant seed rain (Woodall 1982, Hofstetter 1991). The viability and propensity for canopy-held melaleuca seeds to germinate declines as the seeds age (Meskimen 1962, Rayachhetry et al. 1998). Seed germination is facilitated by both alternating wet and dry cycles and continuous wet conditions (Myers 1975). About 2% of viable seeds exhibit either inherent or induced dormancy (Rayachhetry et al. 1998) despite exposure to optimal conditions for germination. These dormant seeds incrementally contribute to the soil seed bank. A small fraction of seeds remain viable in dry sites even after 2 years in the soil (T. K. Van and M. B. Rayamajhi, unpublished data).

Unfortunately, none of the above information exists for trees growing in Australia, despite the fact that the conservation of melaleuca is a subject of concern there (Greenway 1994, Turner et al. 1998). Therefore, it is not known whether the expression of these invasive attributes in the adventive range is due to release from repressive factors or whether the recipient habitats are less resistant to invasion. In order to gain insight into this, we compared biological attributes of canopy-held melaleuca seed-capsules and seeds between southern Florida, U.S. (henceforth, the U.S.) and northeastern Australia (henceforth, Australia). Our specific objectives were to assess seed quality and quantity in both places. This assessment should reveal the regenerative potential of melaleuca trees in Australia and the U.S.

MATERIALS AND METHODS

Sample Trees: During 1996 to 1997 and 1999, seed-capsule bearing branches from melaleuca trees growing in non-aquatic, i.e., dry and seasonally flooded habitats in Broward, Dade, and Collier counties of Florida, U.S., were sampled for infructescense (capsule-cluster) attributes and seed qualities. Seed-capsule bearing branches of melaleuca trees from non-aquatic habitats of southern Queensland and northeastern New South Wales in Australia were sampled only during 1999. A total of 15 and 23 trees (height >5 m) were sampled for U.S. and Australia, respectively. To obtain the greatest number of linearly aligned infructescence positions, sample trees were selected from the edge of mature stands or from open roadsides.

Infructescense Attributes: In total, 231 and 43 mature infructescences were harvested from trees in the U.S. and Australia, respectively. The length of each infructescence was measured and capsules were detached from the axis and counted. All capsules collected from each tree were then mixed, and 4 capsules per tree from the Australian trees (total 60 capsules) and 25 capsules per tree from the U.S. trees (total 425 capsules) were randomly selected. Each capsule was individually placed in a small plastic container and air dried at 28 to 35C for 7 d before extracting, counting, and weighing the seeds.

Seed Quality: Branches bearing visibly higher numbers of infructescence positions on sample trees were harvested. Infructescences occupying similar positions on branches within a tree were considered as the same age cohort. Adjacent infructescences, located on the same stem axis were considered distinct if they were separated by a series of leaves or bud scales. Due to indeterminate growth of the flowering branches, infructescences located more proximally to the main stem were considered older than those located more distally (Briggs and Johnson 1979). Each series of infructescences was followed proximally along a sample branch until no older infructescences were present. There were as many as seven linearly positioned infructescences, i.e., seven age cohorts, on branches of some trees. The youngest infructescences positioned near branch tips were designated as Infructescence I, while the oldest infructescences positioned near trunk or main branch were designated as Infructescence VII. Even though trees were selected to provide the maximum number of cohorts, all trees did not possess all cohorts. Only a few branches carried more than three infructescence positions.

When present, at least five infructescences per age cohort per tree (one from each of the five branches) were harvested and infructescences representing different age cohorts within a tree were placed in different plastic bags and marked accordingly. These plastic bags were opened and air-dried in greenhouse or drying oven at 25 to 40C for 3 to 7 d. Seeds from some young capsules (usually from Infructescence I) had to be released by mechanical disruption of the capsule lid, but older capsules dehisced readily on their own and released seeds within 2 to 3 d. Seeds obtained from the infructescences in different age cohorts were placed in different plastic bags, sealed, and stored at room temperature (ca. 25C) for use in the experiments described below.

Seed fill (seed containing an embryo or endosperm, hereafter referred to as embryonic seed), viability, and germinability were studied using methods reported by Rayachhetry et al. (1998). Seeds containing living embryos were stained cherry red with 2,3,5,-triphenol tetrazolium chloride (TTC) (Grabe 1970) and were counted as viable. A viable seed was considered to be germinable if the radicle was visibly emerging from the seed coat after soaking in water or TTC (Rayachhetry et al. 1998). Treated seeds containing pink or glassy-white contents were considered non-viable and hence non-germinable (Grabe 1970, Rayachhetry et al. 1998).

Four samples from Australia and two from the U.S. containing 200 seeds each were chosen randomly from a stock of several thousand seeds in each infructescence-cohort-position per tree. Thus, there were at least 60 and 46 petri dishes each containing 200 seeds that represented the number of replications for each of the first three infructescence positions (Infructescences I, II, and III) in Australia and the U.S., respectively. Replications of the remaining infructescence positions varied from 4 to 44 in Australia and 10 to 47 in the U.S., depending on the availability of the particular cohort.

Each sample of 200 seeds was evenly spread onto a sterile filter-paper pad in a 8.5-cm diameter petri dish and soaked with 3-ml sterile water or TTC (Rayachhetry et al. 1998). These petri dishes were then closed, sealed with Parafilm®, and placed in a dark cabinet drawer at room temperature (ca. 25C). After 10 and 14 d, the petri dishes were removed from the dark and the seeds were examined using a dissecting microscope to determine if they were embryonic, viable, and germinating. Embryonic seeds soaked in either sterile

distilled water (SDW) or TTC appeared non-transparent when viewed with back lighting. The TTC-treated seeds were classified as non-stained, pink or cherry red. Presence or absence of embryos and color development in TTC-treated seeds were verified by rupturing the seed coats.

Data Analyses: Data were analyzed using GLM procedures (SAS 1985). Arcsine transformed percentages of seed fill, viability, and germination were analyzed using one-way analysis of variance with country (Australia or U.S.) as an independent variable. Furthermore, arc- sine transformed data within each country were analyzed using one-way analysis of variance with infructescense-position as independent variable. Differences among treatments were determined using Fisher's protected least significant difference (LSD) test.

RESULTS

Infructescence Attributes: Twigs and branches of isolated melaleuca trees in both Australia and the U.S. contained up to seven visibly discernable infructescences along the linear length of a given branch. Analyses of variance showed differences in infructescence attributes between Australia and the U.S. (Tables 1 and 2). Infructescence lengths were similar (P= 0.0851) in Australia (5.7 cm) and the U.S. (6.0 cm). Mean capsule density in infructescence (capsules per unit axis-length) was higher on the trees from the U.S. than on the trees from Australia (P = 0.0001), but the numbers of seeds per capsule were similar (P = 0.5449) in both areas. Scars of aborted flowers or capsules on infructescence axes were more frequent in Australia than in the U.S. Total seed content in an average infructescence was estimated to be 4,878 in Australia as compared to 12,936 in the U.S. Of these, only 161 seeds were estimated to be viable in Australia, compared to 1,203 in the U.S.

Seed Quality: Physical characteristics of TTC-treated empty, embryonic, viable and germinable seeds from both Australia and the U.S. were similar to those described for the U.S. by Rayachhetry et al. (1998). Seed coats of embryonic seeds were permeable to water, and became soft after soaking for a few hours. Empty seeds remained brittle even after soaking for 10 d. Embryonic seeds were relatively cylindrical and some remained unstained while others stained either cherry red or light pink. Unstained and light pink embryos did not germinate and so were considered non-viable. Seeds staining cherry red consistently demonstrated epigeal germination.

Analyses of variance of the seed attributes showed differences in seed qualities between Australia and the U.S. (Table 1). Overall, seed quality was reduced in Australia relative to the U.S. (Table 3). Embryonic seeds comprised 9% vs 14% of the total seed crop, viable seeds 3% vs 9%, and germinated seeds 3% vs 8% in Australia vs the U.S., respectively. Similarly, viability (39%) and germination (34%) of embryonic seeds in Australia were significantly less than the viability (63%) and germination (52%) of embryonic seeds in the U.S. (Table 3). However, the germination percentages of viable seeds were similar in both Australia and the U.S.

In general, quality of seeds in different infructescence positions differed in both Australia and the U.S. (Table 4). In Australia, the proportion of embryonic seeds was least in Infructescence IV while viability and germinability was least in Infructescence VI and greatest in Infructescences I to III. Embryonic seeds in Australia had similar viability and germinability proportions across Infructescences I to VI, and so was the germinability trends of viable seeds in infructescences. In the U.S., the proportion of seeds with embryos and their viability and germinability was least in Infructescences I and VII and greatest in Infructescences II to IV; similar trends were also observed in viability and germinability of the seeds that were identified as being embryonic. Also, the analysis of viable seeds in the U.S. showed the greatest germinability of seeds obtained from Infructescences II to IV.

DISCUSSION

A maximum of seven successive infructescences were observed on branches of melaleuca trees in both Australia and the U.S., and the infructescence lengths were similar in both geographical areas. An estimation based on data from Tables 2 and 3 showed that the number of capsules and seeds per infructescence from Australia were ca. 34% of that for the U.S. Therefore, number of viable seeds per infructescence in Australia was ca.17% of those in the U.S. These data and the abundant flower or seed-capsule scars observed on the plant samples from Australia suggest that high levels of flower or capsule abortion occur in the natural range of melaleuca. If the total number of infructescences on similar-size trees is

TABLE 1. ANALYSES OF VARIANCE FOR THE EFFECTS OF LOCATIONS (AUSTRALIA VS U.S.) ON MELALEUCA INFRUCTESCENCES, SEED-CAPSULES, AND SEEDS.

Dependent variables*		ms	F	PR > F
Infructescence attributes	Length (cm)	394.00	3.00	0.0850
	Number of capsules per infructescence	17,766.00	125.00	0.0001
	Number of capsules per cm	477.00	135.70	0.0001
	Number of seeds per capsule	2,664.38	0.37	0.5449
Seed attributes	Total embryonic (%)	2,720.94	46.72	0.0001
	Viable of total (%)	3,950.17	105.15	0.0001
	Germinable of total (%)	2,640.41	73.51	0.0001
	Viable of embryonic (%)	63,273.04	65.36	0.0001
	Germinable of embryonic (%)	39,969.89	38.69	0.0001
	Germinable of viable (%)	6,154.44	4.31	0.0384

*df (degree of freedom for the independent variable "location") = 1.

TABLE 2. INFRUCTESCENCE ATTRIBUTES AND NUMBER OF SEEDS PER CAPSULE ON MELALEUCA IN AUSTRALIA AND THE U.S.

Variable		Australia[a]	U.S.[a]
Infructescences[b]	Infructescence length (cm)	5.7 (±1.6) a	6.0 (±1.3) a
	Total number of capsules	18.0 (±13.0) b	49.0 (±17.0) a
	Number of capsules per cm	3.0 (±0.2) b	8.0 (±0.3) a
Seeds per capsule[c]	Numbers	271.0 (±60.0) a	264.0 (±39.0) a
	Dry weight (mg)	Not available	6.6 (±1.9)

[a]Means presented with standard deviations within a row with the same letters are not significantly different at P = 0.05, according to Fisher's protected least significance difference (LSD) test.
[b]N = 231 (Australia) and 43 (U.S.) for "infructescences".
[c]N = 60 (Australia) and 428 (U.S.) for "seeds per capsule".

comparable, then the total seed production of melaleuca trees would be much reduced in Australia compared to the U.S. This assumes a lack of compensatory mechanisms that enable production of several times more capsules per tree in Australia. Field observations suggest that the total capsule numbers per tree are actually much fewer in Australia than in the U.S., which would further accentuate these differences, but additional research is required.

The similarity in the number of melaleuca seeds per capsule in both geographical regions suggest that the initiation and development of ovules into seeds were similar in both Australia and the U.S. Additionally, the overall percentages of embryonic, viable, and germinating seeds were significantly lower in Australia than in the U.S., but germination of viable seeds was similar. Therefore, the percentage of healthy embryonic seeds, capable of initiating seedlings, may be significantly lower in Australia than in the U.S. Weiss and Milton (1984) report a similar reduction in the reproductive performance of *Chrysanthemoides monilifera* (L.) Norlindh (native to South Africa) and *Acacia longifolia* (Andrews) Willd. (native to Australia) in their native ranges when compared to the adventive ranges. Various investigators attribute enhanced reproductive performances in adventive ranges to the lack of natural enemies and inferior competitiveness of associated native plant species (Mothershead and Marquis 2000, Weiss and Milton 1984). Several authors suggest that human alteration of natural systems, melaleuca's inherent biological characteristics, and the lack of natural enemies in North America might be responsible for its explosive invasion of Florida habitats in the U.S. (Hofstetter 1991, Kaufman and Smouse 2001, Myers 1984, Rayachhetry et al. 2001, Turner et al. 1998).

TABLE 3. COMPARISON OF MELALEUCA SEED ATTRIBUTES IN AUSTRALIA AND THE U.S.

Variables	Australia (N = 276)	U.S. (N = 188)
	Mean percentages (standard deviations)[a]	
Embryonic of total	9.0 (±5.4) b	14.0 (±10.1) a
Viable of total	3.3 (±3.3) b	9.3 (±8.8) a
Germinable of total	2.8 (±3.1) b	7.6 (±8.6) a
Viable of embryonic	39.1 (±30.4) b	62.9 (±32.1) a
Germinable of embryonic	34.1 (±37.3) b	51.6 (±35.0) a
Germinable of viable	66.8 (±39.6) a	74.3 (±35.0) a

[a]Means presented with standard deviations in parentheses within a row with the same letters are not significantly different at P = 0.05, according to Fisher's protected least significance difference (LSD) test.

Water and minerals absorbed by roots move to leaves, flowers, and fruits through xylem elements while the carbohydrates and other nutrients are translocated to developing fruits and seeds through the phloem (Stephenson 1981). Logically, any condition that disrupts the manufacture and transport of these nutrients would accelerate the abortion of premature fruits and seeds. Therefore, it may be hypothesized that constant pressure exerted by herbivorous insects and pathogens on vegetative buds, reproductive buds, leaves, stems, and roots of melaleuca reduces net photosynthesis and forces the diversion of photosynthate into the regeneration and replacement of injured tissues. For example, repeated removal or injury of the foliage may in turn reduce total transpiration and indirectly affect the flow of water and minerals through vascular elements. Such actions could suppress flowering or promote premature flower bud and fruit abscissions in melaleuca. Reduced leaf area has been reported to increase fruit abortion in other plant species (Stephenson 1981). Florivores reduced fruit set by 68% in *Oenothera macrocarpa* (Mothershead and Marquis 2000). Janzen (1971) reported that a *Cassia grandis* stand in Costa Rica aborted ca. 95% of the initiated fruits, 85% of which had been damaged by insects (Janzen 1971).

The causes of and mechanisms for capsule abortion, and inferior seed quality in melaleuca are not well understood. Hofstetter (1991) reported that disruption of the vascular tissues that connect the fruits with the stems induced seed release in melaleuca. The proportion of aborted melaleuca flowers and fruits in relation to the total number of flowers initiated is not known in either Australia or the U.S. However, the impact of herbivory on the Australian melaleuca may be substantiated based on surveys by Balciunas et al. (1994), who reported >400 herbivorous insects associated with melaleuca in Australia. Of these, *Oxyops vitiosa* Pascoe (a foliage feeding weevil) released in Florida in 1997 has successfully established on melaleuca populations in most dry and seasonally flooded sites (Center et al. 2000), and preliminary data indicate that defoliation of stem tips by this insect leads to a dramatic reduction in flowering and seed production (Pratt, unpublished data).

TABLE 4. EFFECT OF INFRUCTESCENCE POSITION ON MELALEUCA SEED ATTRIBUTES IN AUSTRALIA AND THE U.S.

Variables	Infructescence positions						
	I	II	III	IV	V	VI	VII
Australia (N = 4-62)[a]							
Embryonic of total	8.9 ab	8.2 ab	9.9 ab	7.7 b	10.6 ab	8.9 ab	11.6 a
Viable of total	3.1 abc	3.5 ab	4.8 a	2.2 bc	3.1 abc	1.2 c	3.1 abc
Germinable of total	2.5 abc	2.7 abc	4.3 a	1.9 bc	2.5 abc	0.8 c	3.0 ab
Viable of embryonic	33.0 ab	46.3 a	45.6 a	41.9 a	31.2 ab	20.3 b	27.6 ab
Germinable of embryonic	28.7 a	43.2 a	40.5 a	33.6 a	25.9 a	18.3 a	27.1 a
Germinable of viable	59.5 b	67.6 b	76.4 ab	68.1 b	63.6 b	52.7 b	97.7 a
U.S. (N = 10-47)[a]							
Embryonic of total	12.8 ab	14.3 ab	16.2 a	16.7 a	12.3 ab	11.8 ab	9.0 b
Viable of total	8.2 abc	10.5 ab	12.4 a	11.8 ab	6.8 bcd	4.1 dc	1.6 d
Germinable of total	3.7 c	9.9 ab	11.5 a	11.1 a	5.9 bc	3.3 c	1.2 c
Viable of embryonic	68.9 a	76.5 a	65.7 a	67.1 a	52.4 ab	34.7 bc	18.3 c
Germinable of embryonic	34.1 dc	67.2 a	66.5 ab	63.7 ab	47.7 bc	27.6 dc	14.2 d
Germinable of viable	63.9 c	91.1 a	85.4 a	86.2 a	70.9 ab	61.4 bc	60.0 bc

[a]Means (%) within a row with the same letters are not significantly different at P = 0.05, according to Fisher's protected least significance difference (LSD).

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