Dispersal potential of *Scaevola crassifolia* (Goodeniaceae) is influenced by intraspecific variation in fruit morphology along a latitudinal environmental gradient

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Abstract. Dispersal of plant propagules by ocean currents can result in long-distance dispersal and is important for the persistence of coastal species. However, the ability of such species to disperse via the ocean is often unknown because there is relatively little evidence that demonstrates that seeds or fruits can float and survive for extended periods in seawater. Furthermore, the seed or fruit traits, and intraspecific variation in these traits, that facilitate buoyancy remain largely unidentified. The genus *Scaevola* (L.) contains several widespread coastal species that may be capable of oceanic dispersal, such as *S. crassifolia* (Labill). We collected fruits of *S. crassifolia* along 700 km of a latitudinal environmental gradient. These fruits were used to determine the influence of fruit morphology and anatomy on fruit buoyancy. Morphological and anatomical variation in *S. crassifolia* was associated with dispersal potential. Our empirical data demonstrated that fruits with larger aeriferous mesocarp layers have greater buoyancy and, therefore, enhanced capacity for long range oceanic dispersal. Of three characters hypothesised to affect buoyancy (aeriferous mesocarp, air pockets in empty locules, and number of vascular cavities), only the properties of the mesocarp were significant. Intraspecific variation can significantly affect dispersal potential, and should not be overlooked in dispersal ecology.

Introduction

Seed dispersal is crucial to the formation and persistence of plant populations, and hydrochory (dispersal by water) is increasingly recognised as an important dispersal mechanism. Hydrochory, as with other dispersal mechanisms, significantly affects patterns and processes at genetic (e.g. gene flow and diversity), community (e.g. species richness and arrival of new species) and population (e.g. longevity and range size) levels (Nilsson *et al*. 2010). Capacity to undertake long-distance dispersal is likely to be increasingly important for the persistence of plant species as their ranges shift in response to continuing global climate change (Hughes 2000; Travis *et al*. 2013). Dispersal via ocean currents can potentially result in long-distance dispersal, with recent phylogenetic and biogeographic studies leading to a resurgence of support for oceanic hydrochory as a means of long-distance dispersal of plants (Howarth *et al*. 2003; de Queiroz 2005; Cousens *et al*. 2008; Dawson and Hamner 2008; Kokubugata *et al*. 2012). However, unlike Darwin's seminal studies of oceanic

hydrochory (Darwin 1856, 1859), recent hypotheses are generally not supported by evidence that fruits or seeds are capable of remaining buoyant and surviving in seawater for the extended periods required to achieve effective long-distance dispersal.

Buoyancy is a key factor that governs hydrochorous dispersal of seeds, which may be associated with intraspecific variation in morphological and anatomical traits of the dispersal unit (Lopez 2001; Leyer and Pross 2009; Vargas *et al*. 2014). However, differences in the morphology of seeds or fruits within a species may also influence dispersal capacity (Darling *et al*. 2008). Such variation may arise through genetic variation, the location of fruits in the infructescence, or the maternal environment during fruit development and maturation (Matilla *et al*. 2005; Donohue 2009). Such variation in seed or fruit morphology may greatly affect the dispersal potential of seeds (Darling *et al*. 2008). For example, infraspecific variation in subspecies of *Bolboschoenus maritimus* (L.) (Cyperaceae) affects the duration of achene buoyancy (Hroudova *et al*. 1997). *B. maritimus* subsp.

compactus possesses well developed aeriferous tissue in the exocarp, resulting in greater buoyancy than the achenes of *B. maritimus* subsp. *maritimus*, which have thin or no aeriferous tissue in the exocarp (Hroudova *et al.* 1997). Further, the effect of intraspecific variation can be evident in seeds from the same parent plant. For example, at low wind speeds, the dispersal distance of winged seeds of *Spergularia marina* (L.) (Caryophyllaceae) was greater than that of seeds without wings, whereas in water, winged seeds were more frequently trapped in vegetation than seeds without wings (Telenius and Torstensson 1989). At a time when metadata analysis and multispecies models are increasingly common, intraspecific variation is often overlooked despite the potential to influence the frequency of rare events such as long-distance dispersal.

Intraspecific variation in seeds and fruits has been linked to differences in dispersal capacity and used to identify specific traits associated with large dispersal distances. Manipulation of seeds or fruits, or the construction of mimics (artificial seeds or fruits), is one method of investigating relationships between dispersal and intraspecific variation in seed or fruit traits such as mass, area and the presence of appendages (Augspurger and Franson 1987; Hughes and Westoby 1992; Yang *et al.* 2012). Although many seed and fruit traits are frequently proposed to be associated with particular dispersal vectors, the traits associated with hydrochorous dispersal have rarely been demonstrated experimentally. Seed characteristics associated with air chambers are commonly assumed to result in extended buoyancy (Higgins *et al.* 2003; Cousens *et al.* 2008) and some investigations have determined the particular traits that influence buoyancy in a small number of plant species. For example, aeriferous tissue in the exocarp of *Bolboschoenus* (Cyperaceae) (Hroudova *et al.* 1997), low specific weight (mass/volume) of 12 species from Panama (Lopez 2001), and the volume of an air pocket between embryonic cotyledons in *Swartzia* (Fabaceae) seeds (Williamson *et al.* 1999) are all associated with prolonged buoyancy. The effect of morphological traits on buoyancy requires further investigation, particularly for species that have diaspore morphologies different from those of the few species that have been studied.

The majority of Goodeniaceae genera are confined to the Australian continent, except for *Scaevola*, which is pantropical; 40 of 130 species are found outside Australia (Howarth *et al.* 2003). These species occur throughout the coastal regions of the Pacific and Indian Oceans, including the tropical Americas, Africa, Philippines, China, Marquesas and Hawaiian Islands (Howarth *et al.* 2003). Phylogenetic relationships within *Scaevola* suggest three independent colonisation events from the Australian continent to the isolated Hawaiian Islands (Howarth *et al.* 2003). This finding, combined with widespread distributions of several *Scaevola* species, implies a capacity for long-distance dispersal in *Scaevola*. This capacity may result from or be enhanced by fruit morphology. For example, it has been hypothesised that the widespread distribution of *S. taccada* may be due to its fleshy exocarp (facilitating bird dispersal), or its corky mesocarp (facilitating buoyancy in water) (Lesko and Walker 1969; Howarth *et al.* 2003). Certainly, the fruits of the widely distributed *S. crassifolia* and *S. taccada* are buoyant

and survive in seawater for 42 and 120 days, respectively, without adverse effects on seed germination, demonstrating a capacity for oceanic dispersal (Lesko and Walker 1969; Guja *et al.* 2010).

The aeriferous, cork-like fruit coat of *Scaevola* species is often identified as a key trait that may determine oceanic dispersal ability (Lesko and Walker 1969; Howarth *et al.* 2003). However, there have been no experimental investigations of the capacity of the aeriferous fruit coat, or intraspecific variation in fruit morphology, to influence buoyancy. Fruits of all *Scaevola* species are indehiscent and drupe-like, with a hard endocarp towards the locules (Carolin 1966). Three layers are visible in most species and are referred to as epicarp, mesocarp and endocarp, although they do not correspond exactly to the layers as named in true drupes because the epicarp is likely to be derived from outer floral whorls rather than ovary tissue (drupe-like, cf. Carolin 1966). In fruits of *S. crassifolia*, the endocarp and mesocarp are not differentiated and are, henceforth, referred to as mesocarp. Unlike some *Scaevola* species that have succulent or fleshy epicarp and mesocarp layers, *S. crassifolia* fruits are dry with gradation to unthickened cells on the outermost part of the fruit (Carolin 1966). The outer mesocarp consists of air-filled parenchyma cells, which in some species is presumed to be the feature most likely to promote buoyancy (Lesko and Walker 1969; Howarth *et al.* 2003). Fruits of *S. crassifolia* have two (Carolin 1966), or occasionally three locules (L. K. Guja, pers. obs.). Often only one locule is filled (L. K. Guja, pers. obs.) and the resultant air pocket in the empty locule, surrounded by hard, dry mesocarp, may increase fruit buoyancy. False locules, and small cavities in the mesocarp, are formed by disintegration of vascular bundles (Carolin 1966) and these air pockets may also influence fruit buoyancy.

In the present study, we aimed to identify the anatomical features of *Scaevola* fruits that are most strongly associated with buoyancy, and to test for relationships between buoyancy and intraspecific morphological variation in fruits. We reasoned that the fruits of *S. crassifolia* possess the following three main anatomical traits that may be related to buoyancy: (1) aeriferous mesocarp, (2) air pockets in empty locules and (3) vascular cavities. We quantified anatomical and morphological variation of fruits along a latitudinal environmental gradient and investigated how this variation affected dispersal potential. Specifically, we hypothesised that (1) the anatomical structure of fruits would affect buoyancy, such that fruits with large aeriferous mesocarp and many vascular cavities would be most buoyant, and (2) fruits containing one seed and one empty locule would be more buoyant than fruits containing two filled locules.

Materials and methods

Study species and sites

Scaevola crassifolia is a shrub 0.1–1.5 m high, occurring on frontal coastal sand dunes and limestone cliffs in western and southern Australia (Western Australian Herbarium 1998; Rippey and Rowland 2004; Dixon 2011). The inflorescence is a terminal to subterminal spike of blue/mauve/white flowers present from July to February (Western Australian Herbarium 1998; Dixon 2011; Rippey and Rowland 2004). Fruits are more

or less spherical, slightly compressed, hard, woody and minutely hairy (Marchant *et al*. 1987). The north–south distribution of *S. crassifolia* along the south-western Australian coastline extends for ~2000 km along a strong temperature and rainfall gradient – dry and hot in the north, to wet and cool in the south (Bureau of Meteorology 2013; CSIRO 2013). To examine morphological variation of fruits, collections of *S. crassifolia* fruits were made at eight distant localities along 700 km of the latitudinal temperature and rainfall gradient (Fig. 1). Average annual rainfall at the study sites is 400 mm in the north and 1200 mm in the south (Bureau of Meteorology 2013), and average annual daily mean temperature ranges from 21°C in the north to 15°C in the south (Bureau of Meteorology 2013). Climate data are based on 30-year climatology (1961–1990).

Fruit collection

Mature fruits (browned, woody, dry and easily detached with minimal force) were collected at the natural point of dispersal along the length of multiple infructescences from at least 10 plants at each site between January and April 2009. The average number of fruits collected per site was 23 000 (min 9750 at Breton Bay and max 39 000 at Tim's Thicket). Herbarium vouchers for each collection were lodged at the Kings Park and Botanic Garden Herbarium (KPBG). Collector's field numbers are Coronation Beach LKG003, Dongara LKG024, Scarborough LKG107, Sandy Cape LKG031, Breton Bay LKG060, Tim's Thicket LKG066, Injidup LKG078, Skippy Rock LKG090. At the northern-most site, Coronation Beach, several fruits at the basal end of infructescences had already been released at the time of collection and only some fruits remained at the distal end. Fruits were stored within 2 days of collection in a controlled-environment room at 15°C and 15% relative humidity (RH). After 5 months of storage, when all fruits had equilibrated to 15% RH, fruits were then sealed in laminated aluminium-foil bags and stored at −18°C until used in experiments.

Sample selection

To identify fruits that comprised zero, one or two seeds, fruits were imaged using a digital X-ray (Faxitron MX-20, Faxitron X-ray, Lincolnshire, IL, USA). Fruits from each collection site were mounted upright on double-sided tape so that both locules were visible in X-ray images. For buoyancy experiments and subsequent morphological and anatomical measurements, 30 single-seeded fruits (three replicates of 10) were selected randomly from each collection. For the second experiment, a comparison of buoyancy of one- and two-seeded fruits, samples from all sites were pooled, X-rayed as above, and one- and two- seeded fruits (three replicates of 20 each) were randomly selected. Fruits containing more than two locules were rare and were not used in experiments.

Buoyancy of fruits

To determine buoyancy of fruits from each collection site, three replicates of 10 dry fruits were placed in 250 mL of seawater in plastic containers (11 cm in diameter, 4 cm high, Genfac Plastics, Melbourne, Victoria, Australia). To release surface tension, the water in each container was initially stirred for 30 s (Day 0). During the experiment, the container was topped up with deionised water to balance losses from evaporation and during this process all fruits were agitated (modified from Guja *et al*. 2010). The same procedure was followed to determine buoyancy of fruits containing one or two seeds for each replicate of 20 fruits (pooled across all sites). For both experiments, the number of buoyant fruits was recorded at 0, 3, 6 and 8 days, after stirring. After 8 days, ~50% of fruits remained buoyant and the experiment was terminated so that the buoyant and non-buoyant sample sizes were approximately equal for analysis.

Fruit morphology and anatomy

To study variation in the anatomical features of fruits from each site, sunken and buoyant fruits were removed from seawater,
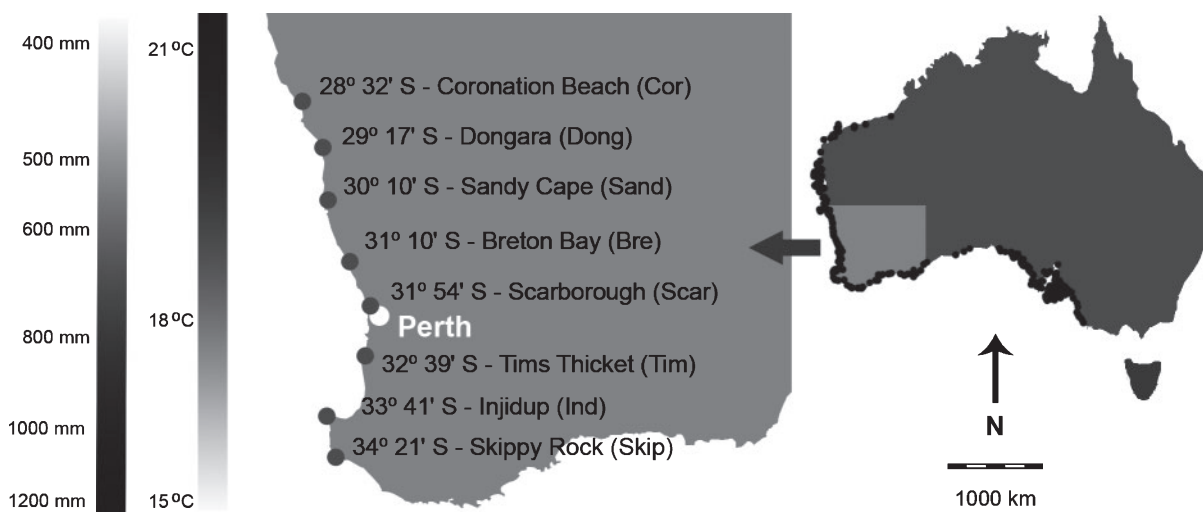
Fig. 1. Map of south-western Australia, showing the study sites for *Scaevola crassifolia*, and the annual average daily mean temperature and mean annual precipitation for coastal localities, as derived from the Bureau of Meteorology (2013). The capital city, Perth, is marked for reference. Abbreviations (in parentheses) are used in reference to each collection location throughout the text. The pericontinental distribution of *Scaevola crassifolia* is represented by black circles in the map on the right (CSIRO 2013).
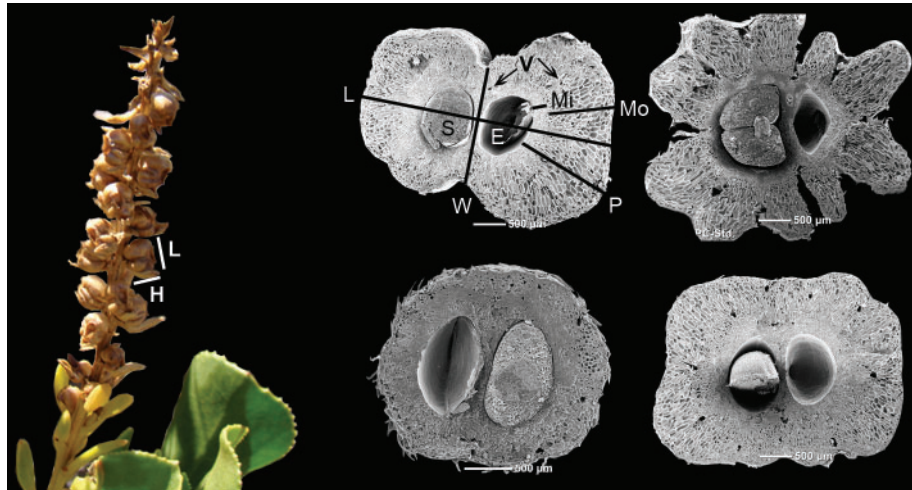
Fig. 2. Infructescence of *Scaevola crassifolia*, identifying the measured height (H) and length (L) dimensions of a fruit (left). Transverse sections of *S. crassifolia* fruits (right). Morphological and anatomical variables measured for each fruit were length (L), width (W), pericarp (P), outer mesocarp (Mo), inner mesocarp (Mi) and vascular cavities (V). Each fruit generally contained one seed (S) and one empty locule (E). A typical fruit is shown top left. Extremes of variation in fruit morphology and anatomy are also shown; ridges in the pericarp (top right), small fruits with minimal outer mesocarp layers (bottom left), and large fruits with large outer mesocarp layers and many vascular cavities (bottom right).

separated, and rinsed in deionised water to remove external salt. Fruits from each replicate were then dried by being placed in 10 g of silica gel for 2 days. Each fruit was weighed, height (Fig. 2) was measured with digital callipers, and each fruit was then cut transversely to expose both locules. One half of the section was mounted, with the cut surface facing upward, on carbon tape on an aluminium stub. Before examination in a scanning electron microscope (SEM), stubs were sputter-coated with gold at 25 mA for 2 min (Emitech K550X, Quorum Technologies, Ashford, Kent, UK). Fruits were imaged using a Jeol JCM6000 SEM under vacuum (Jeol, Sydney, NSW, Australia), with an accelerating voltage of 10 kV and magnification between ×28 and ×40, as required.

Measurements of the length (perpendicular to locules) and width (parallel to locules) (Fig. 2) of the fruit cross-section were made using the scaler function on the graphical user interface of the Jeol JCM6000 licenced software. In cross-section, measurements were taken at both the minimum and maximum to record the variation in the width of layers. The maximum and minimum width of the pericarp (from the inside edge of the locule to the outer edge of the epicarp), outer mesocarp (aeriferous cells) and inner mesocarp (hard layer) were measured (Fig. 2). Approximate total fruit volume (mm^3) was calculated using the formula for an ellipsoid sphere ($4/3\pi \times$ length $\times$ width $\times$ height). Specific weight (mg μL^{-1}) was calculated as mass/volume. Average layer width was calculated as (max + min)/2 for each layer. The ratio of outer to inner mesocarp was calculated by dividing the mean of the outer by the mean of the inner mesocarp. The number of distinct vascular cavities in each fruit was counted.

Statistical analysis

To investigate the extent of intraspecific variation in *S. crassifolia* fruits from different collection locations, each morphological and anatomical variable was analysed with ANOVA, with *post hoc* Tukey's multiple comparisons of means (R version 2.15.1, R Foundation for Statistical Computing, Vienna). Differences in mean buoyancy (% after 8 days) of fruits from each collection site were also compared with one-way ANOVA, with *post hoc* Tukey's multiple comparison of means. Where required, data were transformed and checked to ensure they met assumptions of normality and homogeneity of variance (Shapiro–Wilk test). Fruit width and the number of vascular cavities could not be transformed to normal and were therefore not included in the ANOVAs. Non-transformed data are shown in figures and tables.

To determine the effect of morphological and anatomical variables on buoyancy at 8 days, the two groups (buoyant versus sunken) were compared using binomial generalised linear models (GLM) with a logit link function. All variables were analysed because normality was not prerequisite. Binomial GLMs with a logit link function were also used to compare means for buoyancy of one- versus two-seeded fruits at each time.

Results

There were significant differences among all morphological and anatomical traits (that could be transformed to normal) of fruits from different collection locations (Fig. 2, Table 1). *Post hoc* tests revealed that fruits from Coronation Beach (northern-most study site) were generally the smallest and had the smallest length (2.16 ± 0.22 mm), volume (4.43 ± 1.26 mm^3), pericarp (0.43 ± 0.09 mm), outer mesocarp (0.23 ± 0.09 mm) and mesocarp outer inner ratio (1.26 ± 0.52). These fruits were also the densest (highest specific weight 1.09 ± 0.24 mg μL^{-1}) among all sites. Fruits from Dongara (~100 km south of Coronation Beach) were generally the largest and had the greatest mass (7.22 ± 2.53 mg), height (2.72 ± 0.39 mm), pericarp (0.89 ± 0.18 mm), outer mesocarp (0.69 ± 0.16 mm) and mesocarp outer inner ratio (3.95 ± 1.69) among all collections. Variation in fruit morphological and anatomical
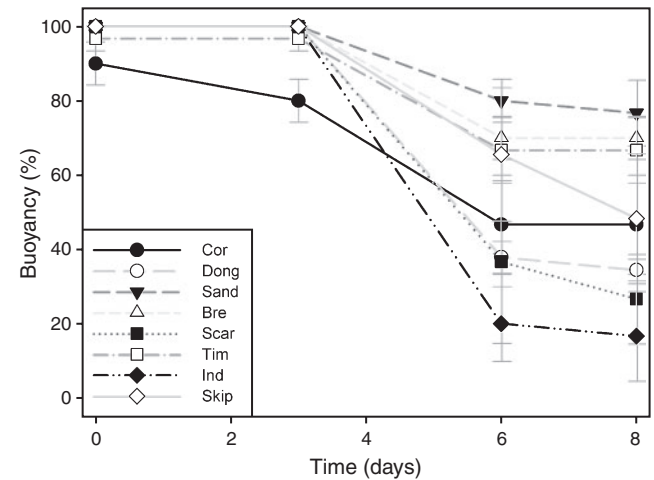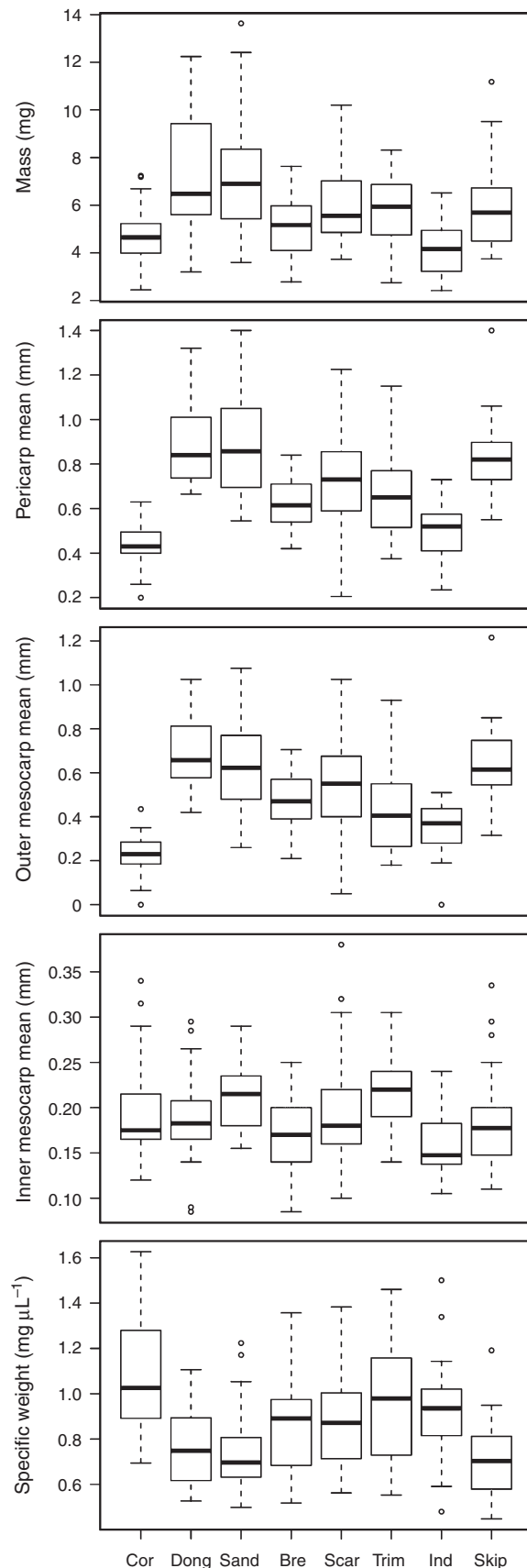
traits (i.e. mass, height, length, volume, specific weight, pericarp mean, outer mesocarp mean and mesocarp outer inner ratio, but not inner mesocarp mean) varied according to collection site, and south from Dongara, there was a general trend of smaller and denser fruits (to Injidup) (Table 1, Fig. 3, selected variables). However, this trend did not extend to the most northern (Coronation Beach) and southern (Skippy Rock) study sites.

Initially, an average of 98% of all fruits were buoyant in seawater. After 8 days, an average of 48% of all fruits remained buoyant. The rate at which fruits sank varied with collection site (Fig. 4). After 8 days, 77% of fruits from Sandy Cape remained buoyant, being the highest percentage among all collection sites, whereas only 17% of fruits from Injidup remained buoyant, being the lowest percentage among all collection sites (Fig. 4). There was no significant difference between buoyancy of single-seeded versus double-seeded fruits at any of the time points investigated (Table 3).

Across all collection locations, many morphological and anatomical variables were significantly different between buoyant and sunken fruits (as separated after 8 days in seawater). Length, volume, pericarp (mean, maximum and minimum), outer mesocarp (mean, maximum and minimum) and mesocarp outer inner ratio were significantly greater in buoyant fruits than in sunken fruits (Table 2). Mean mesocarp thickness was significantly greater for buoyant than for sunken fruits. The 25% and 75% quartiles for the outer mesocarp of buoyant fruits were 0.381 to 0.665 mm ($n = 118$), and 0.281 to 0.600 mm ($n = 112$) for sunken fruits. Buoyant fruits also had a lower specific weight than did sunken fruits (Table 2, Fig. 5). Mass, height, width, inner mesocarp and vascular cavities did not significantly affect fruit buoyancy at 8 days (Table 2).

Discussion

The present study has described large intraspecific variation in the morphology and anatomy of *Scaevola crassifolia* fruits along a latitudinal gradient, and resultant differences in dispersal potential of fruits from each collection site. The basic morphology and anatomical character of fruits was consistent. Yet, as hypothesised, intraspecific variation in the anatomical structure of fruits, particularly the size of the aeriferous outer mesocarp, was related to buoyancy. Here we demonstrated empirically, for the first time, that larger aeriferous mesocarp increases fruit buoyancy and can, therefore, increase the probability and distance of hydrochorous dispersal. These data empirically support propositions made in other studies that aeriferous or cork-like fruit and seed coats increase buoyancy potential (Lopez 2001; Cousens *et al*. 2008; Guja *et al*. 2010; Nilsson *et al*. 2010; Vargas *et al*. 2014). These data also demonstrated that the relationship between aeriferous tissue in the exocarp and buoyancy described for achenes (Hroudova *et al*. 1997) is similar for drupe-like woody fruits with multiple locules. Of the three fruit characteristics expected to affect buoyancy of *S. crassifolia* fruits (aeriferous mesocarp, empty locules and vascular cavities), only the mesocarp differed significantly between buoyant and non-buoyant fruits. A well developed aeriferous outer mesocarp extended the duration of fruit buoyancy, whereas lack of outer mesocarp resulted in denser fruits (high specific weight) that sank rapidly.

Table 1. Morphology and anatomy of fruits collected from each site

Values are means (s.d. in parentheses). For each variable, means followed by the same letter are not significantly different (at $P = 0.05$). The data shown for each of the fruit layers (pericarp, outer mesocarp and inner mesocarp) are the mean calculated from the maximum and minimum widths of the respective layer. Refer to Fig. 1 for explanation of collection-site abbreviations

Collection site	Mass (mg)	Height (mm)	Length (mm)	Volume (mm³)	Specific weight (mg μL⁻¹)	Pericarp (mm)	Outer (mm)	Mesocarp Inner (mm)	Outer : inner	Day 8 buoyancy (%)
Cor	4.66 (1.2)bd	2.12 (0.21)be	2.16 (0.22)f	4.43 (1.26)e	1.09 (0.24)d	0.43 (0.09)e	0.23 (0.09)e	0.20 (0.06)ab	1.26 (0.52)e	46.67 (23.09)ab
Dong	7.22 (2.53)a	2.72 (0.39)a	3.14 (0.44)ab	9.93 (3.97)ab	0.75 (0.16)ab	0.89 (0.18)a	0.69 (0.16)a	0.19 (0.05)ab	3.95 (1.69)a	34.44 (5.09)ab
Sand	7.15 (2.35)a	2.65 (0.30)a	3.39 (0.55)a	10.28 (4.87)a	0.74 (0.19)ab	0.89 (0.24)a	0.63 (0.20)ab	0.21 (0.04)b	2.97 (0.94)abc	76.67 (15.28)a
Bre	5.12 (1.12)bc	2.33 (0.31)bc	2.75 (0.35)cd	6.12 (1.91)cd	0.89 (0.21)bc	0.62 (0.13)bc	0.47 (0.13)cd	0.17 (0.04)ac	2.99 (1.20)abc	70.00 (10.00)ab
Scar	6.00 (1.53)ac	2.57 (0.30)ad	2.94 (0.47)bc	7.36 (2.89)bd	0.87 (0.20)bc	0.72 (0.23)cd	0.52 (0.23)bc	0.20 (0.06)bc	2.81 (1.43)cd	26.67 (20.82)ab
Tim	5.82 (1.52)acd	2.36 (0.23)cd	2.61 (0.43)de	6.70 (2.80)d	0.94 (0.25)cd	0.65 (0.20)c	0.43 (0.21)cd	0.22 (0.04)b	2.06 (0.98)d	66.67 (15.28)ab
Ind	4.12 (1.09)b	2.05 (0.22)e	2.34 (0.37)ef	4.56 (1.40)ce	0.94 (0.21)cd	0.51 (0.12)be	0.35 (0.12)de	0.16 (0.04)a	2.35 (0.97)bd	16.67 (20.82)b
Skip	5.95 (1.82)ac	2.50 (0.27)ac	3.28 (0.39)ab	8.97 (3.59)ab	0.70 (0.17)a	0.84 (0.16)ad	0.64 (0.17)ab	0.19 (0.05)ab	3.72 (1.29)ac	48.15 (30.17)ab
Mean	5.76 (1.99)	2.41 (0.36)	2.83 (0.58)	7.30 (3.71)	0.86 (0.23)	0.69 (0.24)	0.50 (0.22)	0.19 (0.05)	2.76 (1.41)	48.24 (26.07)
ANOVA										
d.f.	7	7	7	7	7	7	7	7	7	7
Test statistic	12.58	21.31	33.86	21.25	11.04	28.99	24.61	5.60	17.92	3.87
P-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0119

Fig. 4. Buoyancy in seawater of fruits (%) from each collection site ($n = 3 \times 10$) over time (days). Vertical error bars represent ± 1 s.e.

Specific weight is often reported to affect buoyancy (Lopez 2001; Cousens *et al.* 2008) and in a multi-species model, it was the only variable that consistently influenced buoyancy over time (L. K. Guja, M. J. Wallace, K. W. Dixon, G. Wardell-Johnson and D. J. Merritt, unpubl. data). In the present study, we have reported for the first time that a larger proportion of aeriferous tissue resulted in *Scaevola* fruits with lower specific weight and this was associated with prolonged buoyancy. The initial high buoyancy of fruits (98%) was likely to be due to their average specific weight being lower (0.9 ± 0.2 mg µL^{-1}) than that of seawater (1.03 mg µL^{-1}). Over extended periods, it is possible that fruits sink over time because of an increase in mass caused by water uptake. Water may be absorbed by the woody fruit coat, or by the seeds imbibing water that has entered through the woody fruit (Turner *et al.* 2009). Future investigations in dispersal ecology should quantify relationships between specific weights of imbibed and dry fruits, and their buoyancy relative to the specific weight of seawater.

Often investigations of dispersal ecology aim to predict dispersal ability, potential or distance by using simple plant, fruit or seed traits (Römermann *et al.* 2005; Will *et al.* 2007; Thomson *et al.* 2010). Hydrochory has received less attention than other dispersal modes, with knowledge of hydrochory in the Australian flora particularly lacking (Thomson *et al.* 2010), even though the continent has a large coastal fringe and numerous wetlands. Whereas we have previously shown that fruits of *S. crassifolia* can survive up to 42 days in seawater and are therefore capable of oceanic dispersal (Guja *et al.* 2010) here we have shown that several morphological variables differ significantly between buoyant and sunken fruits. However, the quantified variables are not all independent. This dependence limited the analysis and required each variable to be assessed individually, preventing the creation of models that account for the relative contributions of different variables to buoyancy

Fig. 3. Box plots of morphological (specific weight and mass) and anatomical variables (pericarp, outer mesocarp, inner mesocarp) of fruits by collection site from left, North (Cor), to right, South (Skip). Refer to Fig. 1 for collection-site abbreviations.

Table 2.   Means (s.d. in parentheses) of morphological and anatomical variables of buoyant and sunken fruits

Significant differences between buoyant and sunken fruits ($P < 0.05$) are identified in bold type and were determined by binomial generalised linear modelling with a logit link function. For all models, there were 228 degrees of freedom

Morphological/anatomical variable	Buoyant		Sunken		Test statistic	*P*-value
Mass (mg)	5.93	(2.01)	5.60	(1.95)	1.27	0.204
Height (mm)	2.44	(0.34)	2.39	(0.38)	1.091	0.275
Length (mm)	2.95	(0.61)	2.71	(0.53)	2.971	**0.00297**
Width (mm)	1.98	(0.46)	1.90	(0.46)	1.288	0.198
Volume (mm^3)	7.84	(3.97)	6.79	(3.39)	2.094	**0.0363**
Specific weight (mg μL^{-1})	0.83	(0.23)	0.90	(0.24)	–2.191	**0.0285**
Pericarp (mm)						
Mean	0.74	(0.24)	0.65	(0.23)	2.602	**0.00926**
Minimum	0.39	(0.20)	0.33	(0.14)	2.693	**0.00708**
Maximum	1.08	(0.35)	0.98	(0.37)	2.087	**0.0369**
Outer mesocarp (mm)						
Mean	0.53	(0.22)	0.46	(0.22)	2.505	**0.0123**
Minimum	0.18	(0.18)	0.12	(0.14)	2.469	**0.0136**
Maximum	0.89	(0.33)	0.80	(0.36)	1.992	**0.0464**
Inner mesocarp (mm)						
Mean	0.19	(0.05)	0.19	(0.06)	–0.559	0.576
Minimum	0.13	(0.04)	0.13	(0.04)	0.343	0.732
Maximum	0.25	(0.06)	0.26	(0.08)	–0.969	0.333
Mesocarp outer : inner	2.95	(1.30)	2.58	(1.49)	1.962	**0.0498**
Vascular cavities	2.71	(2.65)	2.52	(2.57)	0.574	0.566

Table 3.   Mean (s.d. in parentheses) buoyancy (%) of one and two-seeded fruits ($n = 3 \times 20$) in seawater at 0, 3, 6 and 8 days

Buoyancy of one-seeded and two-seeded fruits was not significantly ($P > 0.05$) different as determined by binomial generalised linear modelling with a logit link function. For all models, there were four degrees of freedom

Time	Buoyancy (%)				Test statistic	*P*-value
	One seed		Two seeds			
Day 0	94.82	(5.27)	98.33	(2.89)	0.984	0.325
Day 3	93.07	(8.07)	98.33	(2.89)	1.285	0.199
Day 6	59.12	(11.34)	56.67	(28.43)	–0.293	0.769
Day 8	55.79	(8.84)	56.67	(28.43)	0.081	0.936

Fig. 5. Histogram showing specific weight (mg μL^{-1}) of *Scaevola crassifolia* fruits after 8 days in seawater. The two series, float and sink, indicate the buoyant and sunken fruits. The vertical line at 1.03 marks the density of seawater. Floating fruits are shown in light grey, sunken fruits are shown in intermediate grey, and overlap is shown in dark grey.

potential. Further, the differences between buoyant and sunken fruits do not allow simple prediction of whether a fruit will sink or float. For example, the mean mesocarp thickness of buoyant fruits was significantly larger than that of sinking fruits, although there was also considerable overlap between mesocarp thickness of the two groups. Easily identifiable features of seeds and fruits that are indicative of hydrochorous dispersal remain to be discovered, as do diagnostic traits that would allow identification of buoyant and non-buoyant seeds.

Intraspecific variation can increase dispersal (Augspurger and Franson 1987; Greene and Johnson 1992; Hroudova *et al.* 1997; Higgins *et al.* 2003), affect patterns and processes at genetic, community and population levels (Darling *et al.* 2008; Nilsson *et al.* 2010) and may have ecological consequences, such as risk-spreading, enhancement of population stability and an increase in individual fitness in unpredictable habitats (Andersen 1992). A combination of variation in both seeds (intraspecific variation) and dispersal vectors (environmental variability) affects dispersal distance (Greene and Johnson 1992) and is likely to result in very important, but uncommon, long-distance dispersal events (Nathan 2006; Nathan *et al.* 2008). In the present study,
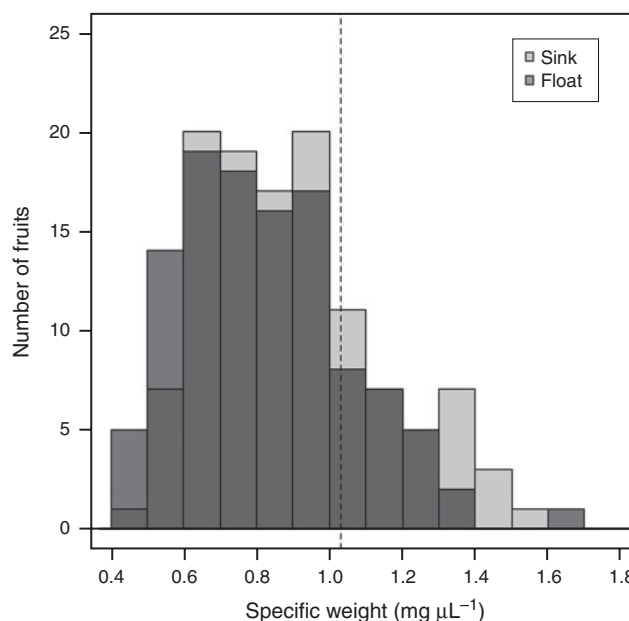
even though intraspecific variation is described along an environmental gradient, it is uncertain whether variation in fruit morphology was driven by genetic or environmental effects or, more likely, by a combination of the two. Environmental variation influencing the maternal environment of the developing seed can affect seed germination, dormancy

and response to environmental conditions or stress (Matilla *et al*. 2005; Donohue 2009). Such effects on germination are critical in a dispersal context because germination in new environmental conditions or under stress will be required for establishment of seedlings post-dispersal. Future research focused on the effects of intraspecific variation on dispersal potential, and germination or stress tolerance, will provide important insights for dispersal ecology. Intraspecific variation that imparts greater buoyancy and establishment potential may facilitate range shifts and assist coastal species to persist through disturbance or other significant changes to local climate.

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