## ORIGINAL ARTICLE

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# Dimorphism of the seed-dispersing organ in a pantropical coastal plant, *Scaevola taccada*: heterogeneous population structures across islands

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Abstract Scaevola taccada is characterized by dimorphic fruits, with one type having cork and pulp (C-morph) and the other type having only pulp (NC-morph). Although within-individual dimorphism has not been observed, both morphs can occur at the same sites. The cork floats on seawater, and the pulp is eaten by birds. Thus, the morphs may have different seed dispersal abilities, via sea currents and birds, respectively. This study aimed to determine the functional characteristics of the dimorphic fruits. First, the potential seed dispersal ability of sea currents and birds was compared between the two fruits morphs by conducting a floating test and by measuring the proportions of different parts of the fruits, respectively. Next, the frequencies of the two morphs across different substrates (beaches, rocks, and cliffs) in the southern islands around Japan were analyzed. Most C-morph fruits remained floating for more than 180 days in a seawater tank, whereas all NC-morph fruits sank after approximately 1 week. The NC-morph fruits had a more pulp volume and less indigestible material than the C-morph fruits. Although both types of plants were found on many islands and all substrates, the C-morph was dominant on beaches, whereas the NC-morph was most frequent on cliffs. The frequencies of the morphs on different substrates might be influenced by the differences in their seed dispersal abilities. The two morphs may differ in fitness on different substrates. These findings improve our understanding of plant adaptations for dispersal.

**Keywords** Coastal plant · Dimorphism · Ecological differentiation · *Scaevola taccada* · Seed dispersal

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#### Introduction

Seed dispersal is important to range expansion by stationary plants. Because individual fitness is related to the ability to reach an appropriate habitat for development and reproduction, the fitness is dependent on the seed dispersal pattern (Rubio de Casas et al. 2012). Seeds and other diaspores are transported away from the parent plant by vectors such as sea currents, animals, and wind (Howe and Smallwood 1982), and their structures are unique to each vector, for example, having cork, pulp, and pappus, respectively. Most fruits can be dispersed by a variety of vectors, although syndromes to increase the propensity of dispersal by specific vectors are observed in nature. For example, plants that are dispersed by sea currents tend to inhabit coastal areas, those dispersed by frugivorous birds inhabit forests, and those that depend on wind dispersal tend to prefer open habitats and forest edges (Howe and Smallwood 1982; Ozinga et al. 2004). Although plants fruit morphology is adapted for effective dispersal by unique vectors, the mechanism by which selection pressure changes the morphology is still not known (Rubio de Casas et al. 2012).

Heteromorphic species that differ in dispersal modes and abilities are good materials for examining the selection process. Dispersal exhibits plasticity to environmental conditions because individuals vary in the proportions of different propagule types (Rubio de Casas et al. 2012). For example, in Crepis sancta (Asteraceae), the ratio of dispersing to non-dispersing propagule types varies with environmental stresses resulting from nutrient depletion and herbivory (Imbert and Ronce 2001). Atriplex sagittata (Chenopodiaceae) produces more dispersing morphs under increased density and nutrient stress conditions (Mandak and Pysek 1999). However, dimorphism in seed dispersal types within a population is not yet known. We report the first such dimorphism, to our knowledge, in Scaevola taccada (Goodeniaceae). Understanding the mechanism that determines this dimorphism might help elucidate the evolution of seed dispersal adaptation.

Scaevola taccada is a coastal pantropical shrub (1–3 m tall) that is distributed along the coasts of the Pacific and Indian oceans. The fruit, which ripens mainly in summer, is a spherical drupe of approximately 10 mm in diameter, which becomes white when ripe (Fig. 1a). This species shows dimorphism in the internal structure of the fruits: one fruit type has endocarp consisting of cork and pulp (C-morph; Fig. 1b, c), while the other type has only pulp (NC-morph; Fig. 1d, e). Such endocarp dimorphism has not previously been reported in S. taccada, which was thought to have only C-morph fruits (Satake et al. 1989; Howarth et al. 2003; Liao 2008). The dimorphism is not distinguishable by appearance, because there is no difference in the external plant characteristics, such as fruits, flowers, leaves, and phenology, although a few individuals of an intermediate morph were found in some populations (Fig. 1f). When all ripe fruits of seven trees (50–232 fruits per tree) were examined for morph type, the trees were clearly either C-morph (three trees) or NCmorph (four trees) (Sakai and Denda, personal data). The cork-morph fruits can float, whereas the NC-morph cannot; thus, the former is thought to have greater hydrochoric dispersal ability than the latter.

In addition, both fruit types are foraged by frugivorous birds, such as the Blue Rock Thrush Monticola solitarius and the Brown-eared Bulbul Hypsipetes amaurotis (C-morph: Kawakami et al. 2009; Emura et al. 2012; NC-morph: Emura, unpublished). However, because the NC-morph fruit has characters adapted for bird dispersal, it may be more useable by frugivorous birds than the C-morph fruit. Birds generally prefer small fruits with small seeds, little indigestible material, and a large edible (pulp) proportion (Alcántara and Rey 2003; Hernández 2009; Gosper and Vivian-Smith 2010). Because the optimal habitats of sea current- and bird-dispersed plants tend to be coastal and inland areas, respectively (Howe and Smallwood 1982), the functional differences between fruit morphs is likely to influence their distributions or frequencies among substrates at different distances from the sea.

In this study, the functional characteristics of fruit dimorphism in this plant was investigated by (1) assessing the floating ability in seawater and by measuring the different parts of the fruits of each morph and (2) comparing the distributions and frequencies of the two morphs in different coastal substrates, specifically beach, rock, and cliff.



**Fig. 1** Two fruit morphs of *S. taccada*. One fruit type having cork and pulp (C-morph) and the other type having only pulp (NC-morph). Both morphs appear identical externally (**a**). The C-morph fruit after removal of half (**b**) and all of the pulp, leaving only the

indigestible part (c). The NC-morph fruit after removal of half (d) and all of the pulp, leaving only the indigestible part (e). Fruit of the intermediate morph after removal of all of the pulp (f)

#### **Materials and methods**

#### Floating test

A floating test was conducted using (1) intact and (2) depulped fruits because these fruits could directly fall from trees to sea in bad weather (high waves and winds), particularly on beaches and because the pulp could be digested by birds and dropped into sea water. For each morph, 100 intact fruits and 430 depulped fruits were used. These fruits were sampled from 10 sites in the Okinawan islands at Okinawajima (OO1, 3, 13, 14, 20–23), Henzajima (OO26), and Ojima (OO28) (Figs. 2 and 3). The depulped fruits were dried naturally for several days before the test. Fruits collected from each site (ca. 50-100 fruits) were soaked in plastic tanks containing 1 L seawater; the number of fruits that sank was counted every 2-3 days. The plastic tanks were shaken at least three times a week to recreate the turbulence of sea currents. Intact fruits were tested for 241 days and depulped fruits for 143 days. Seawater was obtained from a nearby bay and replaced with fresh seawater once every 2 weeks. The hydrochoric potential was estimated by survival analysis (log-rank test) using the survdiff function of the survival package (Therneau 2012) in R (R Core Team 2012). Several C-morph fruits were excluded from the analysis because they refloated after sinking.

## Fruit measurements

We took various measurements from 80 fruits per morph and from approximately ten fruits per tree at one site on

Okinawajima (OO14 in Fig. 3). For each fruit, we measured the volume of pulp, cork, and seed from the width, length, and height of the fruit, depulped fruit, and removed pulp and cork fruit with calipers and used these values to determine the ratio among these three fruit parts for each morph. The mean widths of the indigestible part which is depulped fruit (C-morph; Fig. 1c, NC-morph; Fig. 1e), fruit, and seed were compared between the two morphs using a generalized linear mixed-effect model (GLMM) with Gaussian distribution under maximum likelihood, with pulp volume per fruit, indigestible part, fruit size, and seed size as the response variables; morph type as the fixed effect; and the interaction of fruit morph and intra-individual fruits as a random effect. A model of the pulp volume as the response variable was used with total volume per fruit as the offset term. We performed model selection using Akaike's information criterion (AIC), package lme4 (Bates et al. 2012), and MuMIn (Barton 2013) in R (R Core Team 2012).

Distributions and microhabitats of the two morphs

The frequency of occurrence between the two morphs was surveyed in a total of 4,467 individual trees at 91 sites on 23 islands within south Japan and part of Taiwan (Figs. 2 and 3)—the Sakishima Islands: Ir-iomotejima (SR1–2 in figures), and Uchibanarijima (SR3), Ishigakijima (SI1–13), Taketomijima (SI14–17), Ikemajima (SM1–2), Miyakojima (SM3–10), and Kurumajima (SM11); the Okinawa Islands: Okinawajima (OO1–22), Kourijima (OO24), Ikeijima (OO25), Hamahigajima (OO27), Ojima (OO28), and Agunijima





Fig. 3 Distributions and frequencies of the two morphs of *S. taccada* in the study sites. One fruit type having cork and pulp (C-morph) and the other type having only pulp (NC-morph). Island

(OA1–2); the Amami Islands: Amami-Oshima (AA1–8), Tokunoshima (AT1–6), and Yoronjima (AY1–4); the Daito Islands: Minami-daitojima (DM1–4); the Bonin Islands: Mukojima (BM1), Chichijima (BC1), Minamijima (BC2), and Hahajima (BH1–5). Samples were also collected from the Penghu Islands of Taiwan: Penghu (PP1) and Baisha (PP2). These surveyed islands are located in subtropical regions, which is the northern limit for *S. taccada*.

The seed morph was determined by dissecting ca. 50 fruits from each site. Fewer than 50 fruits were sampled from some sites because of small population sizes and/or inaccessibility due to steep cliffs. This species is occasion-ally classified as having two variants based on the presence or absence of hairs on plant body parts, such as leaves (Satake et al. 1989). However, the variants were not distinguished in this study because the fruit morphs were probably not correlated to the presence or absence of hairs.

The substrate of the study sites was categorized into three coastal types—cliffs, rocks, and beaches

names are abbreviated as in Fig. 2. Asterisks show sampling sites for fruits used in the floating tests

(Fig. 4)—which were determined from a topographical map with a scale of 1:20,000 by using the Digital Japan Web System. The frequency of the two morphs among substrates was compared using a GLMM with a binomial distribution, with occurrence of the NC-morph as the response variable and substrate type as a fixed effect; island was assigned as a random effect. Model fit was tested using a likelihood ratio test. The GLMM was run using the lmer function of the lme4 package (Bates et al. 2012) in R (R Core Team 2012). Individuals of the intermediate morph were excluded from the analysis.

## Results

Comparison of fruit characteristics between the two morphs

The C-morph of both intact and depulped fruits had significantly greater floating ability than the NC-morphs



**Fig. 4** Frequencies of the two morphs of *S. taccada* on different coastal substrates: cliffs (**a**), rocks (**b**), and beaches (**c**). One fruit type having cork and pulp (C-morph) and the other type having

(log-rank test: intact fruit,  $\chi_1^2 = 198$ , p = 0; depulped fruit,  $\chi_1^2 = 980$ , p = 0). In the intact-fruit experiments, 96.0 % of the C-morph fruits floated for more than 150 days, whereas all the NC-morph fruits sank between 6 and 11 days (Fig. 5a). In the depulped fruit experiments, 97.7 % of the C-morph fruits remained floating after 200 days, whereas 72.9 % of the NC-morph sank during the first day, and the remainder had all sunk by 6 days (Fig. 5b). The floating ability was not significantly different between the intact and depulped fruits of the C-morph (log-rank test:  $\chi_1^2 = 0.3$ , p = 0.568), whereas the intact fruits of the NC-morph had significantly better floating ability than the depulped fruits (Log-rank test:  $\chi_1^2 = 410$ , p = 0).

The NC-morph had a larger mean pulp volume per fruit and smaller mean indigestible part width than the C-morph, whereas the mean fruit and seed widths were not different between the morphs (Table 1). The model selection procedure also showed considerable support for the effect of fruit morph on pulp volume per fruit and indigestible part width and no support for that of fruit and seed widths (Table 2).

only pulp (NC-morph). Abbreviations on the x-axis are as in Figs. 2 and 3. The *photographs* show typical study sites for each substrate, and the *graphics* show topographical map symbols

Frequency of the two morphs between islands and substrates

Both morphs occurred throughout the islands and on all substrate types studied. The C-morph was dominant on beaches, whereas the NC-morph was more frequent on cliffs than on other substrate types. The effect of substrate on morph frequency was highly significant (GLMM,  $\chi_3^2 = 717.29$ , p < 0.0001; Fig. 4). Although some sites had only C-morph fruits, there was no site that contained exclusively NC-morph fruits. Sixty-eight individuals at 18 sites on five islands (Okinawajima, Miyakojima, Kurumajima, Ishigakijima, and Taketomijima) showed intermediate morphs, irrespective of substrate type.

## Discussion

We found that the two endocarp morphs of *S. taccada* had clearly different hydrochoric potentials, which could affect their seed dispersal abilities by sea current. Most



Fig. 5 Floating rate (%) of the two morphs of *S. taccada* fruits in sea water. One fruit type having cork and pulp (C-morph) and the other type having only pulp (NC-morph). Intact (a) and depulped (b) fruits were studied

C-morph fruits continued to float on seawater for a long period, whereas all NC-morph fruits sank rapidly. The C-morph seeds retained their ability to germinate even after floating in seawater for 3 months (Lesko and Walker 1969; Nakanishi 1988). This morph can thus disperse over a long distances by sea currents. Seeds of pantropical coastal strand plants can generally float well in seawater (Carlquist 1974). The worldwide coastal distribution of S. taccada might be attributed the long dispersal ability of the C-morph fruits. However, our experiments revealed that NC-morph fruits could not disperse via sea currents as far as the C-morph fruits. Because many NC-morph fruits with pulp floated for only approximately 1 week, they are likely to be dispersed by sea currents only among neighboring beaches. In future studies, we will test whether the NC-morph seeds can germinate before and after floating in sea

water. Because there was no difference in the seed size of the C- and NC-morph fruits, they may have similar germination ability.

The NC-morph fruit had more pulp volume and a smaller indigestible part than the C-morph fruit. Thus, we presume that the NC-morph fruit is foraged to a greater extent by birds and has a higher potential for bird dispersal than the C-morph fruit. Although there was no difference in fruit width between the morphs, their soft pulp was nibbled by small birds, such as Japanese White-eyes Zosterops japonicus, which is common on the studied islands (Emura pers. obs.). This bird would contribute to dispersal of the seeds of NC-morph fruits by swallowing the indigestible part (mean width: 3.93 mm, Table 1), because they can swallow solids < 5 mm in width (Kawakami et al. 2009; Emura et al. 2011). In contrast, shorebirds and seabirds also occasionally forage fruits and are potentially excellent longdistance seed dispersers owing to their long gut pass times and good mobility (Nogales et al. 2001; Calvino-Cancela 2011; Gillespie et al. 2012). The C-morph fruit should be more adapted to these dispersers than the NCmorph fruit, because if it is digested by these birds and dropped into sea water, it would be further dispersed by sea currents. Additional studies are required to identify the animal seed dispersers of the two different morphs. In addition, we must determine whether the morphs appear different to birds, because their color vision is different to that of humans (Siitari et al. 1999), and thus birds might be able to distinguish the two fruit morphs.

The two morphs are common on almost all of the subtropical islands studied. In addition, we found one NC-morph tree on a beach where we observed many C-morph trees in New Caledonia in the southern hemisphere (Emura, pers. obs.). The seed dimorphism might also be widespread. Indeed, many organisms on oceanic islands lose their long-distance dispersal ability after they establish colonies (Carlquist 1974; Roff 1990), as indicated by the genetic analyses of *Hibiscus glaber*, a tree endemic to the Bonin islands, and H. tiliaceus, a pantropical coastal tree (Malvaceae; Takayama et al. 2006; Kudoh et al. 2013). In addition, some weeds have been shown to have decreased seed dispersal ability, with smaller pappus volume and increased achene volume, after they colonized small coastal islands of Vancouver (Cody and Overton 1996). According to a phylogenetic tree of Scaevola based on the ITS region, the closest relatives of S. taccada inhabit the interiors of south Pacific islands: New Caledonia, Fiji, Samoa, Marquesas,

**Table 1** Characteristics of the two fruit morph of *S. taccada*: one fruit type having cork and pulp (C-morph) and the other type having only pulp (NC-morph)

Fruit morph (Number of fruits)	Mean ratio of volume (%)			Mean width $\pm$ SD (mm)		
	Pulp (Digestive)	Cork (Non-digestive)	Seed (Non-digestive)	Non-digestive part	Fruit	Seed
C-morph (80) NC-morph (79)	83.1 93.1	11.6	5.3 6.9	$\begin{array}{c} 6.61 \ \pm \ 0.60 \\ 3.93 \ \pm \ 0.29 \end{array}$	$\begin{array}{rrrr} 11.81 \ \pm \ 1.07 \\ 11.36 \ \pm \ 0.92 \end{array}$	$\begin{array}{r} 3.96 \ \pm \ 0.26 \\ 3.93 \ \pm \ 0.29 \end{array}$

**Table 2** Summary of model ranking using the Akaike information criterion (AIC) to test the effect of fruit morph

Model ranks	Model structure	AIC	ΔΑΙΟ	$w_i$
Pulpe volume p	per fruit			
1	$\sim$ Fruit morph	31,326.2	0.00	1
2	Null	31,355.8	29.60	0
Non-digestive p	oart width	,		
1	$\sim$ Fruit morph	144.0	0.00	1
2	Null	185.8	41.78	0
Fruit width				
1	Null	345.1	0.00	0.6
2	~Fruit morph	346.0	0.86	0.4
Seed width	1			
1	Null	-31.5	0.00	0.7
2	$\sim$ Fruit morph	-29.5	1.94	0.3

Fruit morph means two fruit types, one type having cork and pulp (C-morph) and the other type having only pulp (NC-morph).  $\Delta AIC$  is the delta weight (difference between the AIC for a given model and the best fitting model). wi is the model selection probability (Akaike weights)

and Tahiti (Howarth et al. 2003). These species bear fruit lacking cork, and their seeds are dispersed by birds (Carlquist 1974; Howarth et al. 2003). Their fruit is mostly black, whereas that of *S. taccada* is white. The former would be more appealing to dispersing birds than the latter (Wheelwright and Janson 1985). This evidence suggests that each island-endemic species evolved a fruit morph adapted to bird dispersal during the process of speciation after its C-morph colonized via sea currents. Therefore, the NC-morph might be in an intermediate stage between the C-morph and those of these inland species.

The frequencies of the two morphs was predictably different among coastal substrates, although both the morphs occurred widely. The C-morph was found at a higher frequency on beaches than on other substrates, whereas the NC-morph occurred more commonly on cliffs. For example, among all the study sites, the NCmorph was most dominant in Minami-Daitojima, because this island consists of upheaved coral and is surrounded only by cliffs. Thus, the interaction between morph dispersal ability and substrate has influenced the distributions of the two morphs. Driftage washes up more easily on beaches than on cliffs. Presumably, the fitness of the C-morph on beaches is higher than that of the NC-morph, while that of the NC-morph may be higher on cliffs, where birds rather than sea currents are likely to be main seed dispersers. To test this hypothesis, in future studies, we will need to compare the morphologies of the two fruit morphs and bird preferences among different substrates.

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