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Greenhouse Growth of Native American Beachgrass (*Ammophila breviligulata*) and Invasive Asiatic Sand Sedge (*Carex kobomugi*) Under Competition

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ABSTRACT

Worldwide, dunes buffer peripheral coastal areas from destructive abiotic elements of erosion and storms. Vegetation is a major element of these systems as roots bind sand and thereby, stabilize dunes and shoots promote dune growth. The dunes of the Mid-Atlantic U.S. are stabilized by two alpha species that compete for space and resources-native American Beachgrass (*Ammophila breviligulata*) and invasive Asiatic Sand Sedge (*Carex kobomugi*). Despite the importance of these species, today many of the biological and physiological factors underpinning their competition remain poorly understood. Therefore, we conducted a 7 week greenhouse competition study with transplanted *A. breviligulata* and *C. kobomugi* ramets. We manipulated substrate amount and salt spray as treatments in a factorial-designed greenhouse experiment. Despite ample acclimation prior to testing and appropriate abiotic conditions throughout, we had very low survivorship for both species. This was especially true for *C. kobomugi*, which may be largely intolerant of wet substrate conditions. We performed microscopy to begin to understand the morphological and physiological differences that could have drive differences in our survival rates. Our results provide information useful for the design and uses of future attempts at conducting coastal vegetation transplant studies.

Key words: Coastal dunes, *Carex kobomugi*, *Ammophila breviligulata*, greenhouse, competition

INTRODUCTION

Competition in naturally disturbed areas is inherent in many ecosystems, including coastal dunes. Dunes protect upland infrastructure by buffering against storms, daily wind and wave action. Vegetation is an integral element of a strong dune system because it stabilizes dunes, with its roots and provides an accretion surface via the shoots. Along the Atlantic coast, American beachgrass (*Ammophila breviligulata*); is the native dominant grass stabilizing primary dunes areas. However, since 1929, *A. breviligulata* has been competing for resources and dominance with the invasive Asiatic sand sedge (*Carex kobomugi*).

Carex kobomugi is a perennial graminoid with a guerilla-type clonal growth form that allows it to infiltrate new areas locally (Ishikawa and Kachi, 1998). High seed buoyancy facilitates effective longshore transport to new localities (Yang *et al.*, 2012). Guerilla-type growth species are highly effective at spreading out over wide areas and are hard to eradicate due to their propensity to rapidly propagate asexually via long lateral rhizomes and reestablish via frequent seed dispersal (Hacker *et al.*, 2012).

Stands of *C. kobomugi* form dense, largely continuous and low-lying monoculture mats with little to no space in between individuals (Small, 1954; Wootton *et al.*, 2005) thus crowding out native species atop the dune and in the rhizosphere of the substrate (Burkitt and Wootton, 2010; Ishikawa and Kachi, 1998; Wootton, 2007; Wootton *et al.*, 2005). The *C. kobomugi* has been largely responsible for reduced abundance and density of native plant species along the coast, such as *A. breviligulata* and Seaside Goldenrod (*Solidago sempervirens*) (Wootton *et al.*, 2005). Reducing either functional or species diversity decreases resilience to small and large-scale perturbations (Diaz and Cabido, 2001; Reiss *et al.*, 2009). The reduction of native plants can have resounding short-term effects on organisms, such as the endangered Monarch butterfly (*Danaus plexippus*), which rely on the nectar of *S. sempervirens* during migration (Snell, 2010). *Carex kobomugi* invasion may also render dune space unusable for macro-invertebrates and endangered shorebirds, such as the Piping Plover (*Charadrius melodus*), which rely on open space between dune plants (Woodward and Quinn, 2011).

Conversely, native *A. breviligulata* fosters primary dune diversity (Small, 1954; Wootton *et al.*, 2005). The *C. kobomugi* and *A. breviligulata* are energetically equal as both are perennial graminoid C₃ photosynthesizers but *A. breviligulata* exhibits a phalanx-type growth form. Phalanx growth plants have short distances between ramets (individual members of a clonal community) and slow colonization (Ishikawa and Kachi, 1998). Therefore, *A. breviligulata* is found at much lower densities than *C. kobomugi*, 40 versus 140 ramets², respectively (Reo and Wnek unpublished data; Small, 1954; Wootton *et al.*, 2005). Low levels of intraspecific competition among highly intermingled clonal colonies may allow *C. kobomugi* to expand and exist at such high densities (Ohsako, 2010). *Carex kobomugi* stands are increasing at rates of great concern in affected areas. For example, in parts of New Jersey, populations have increased exponentially and expanded by at least 300% from 1985-2005 (Wootton *et al.*, 2005). Because there is currently no effective method of removing *C. kobomugi*, containment has been the mode of action for coastal management.

The exact mechanism by which *C. kobomugi* overtakes other species, especially its native counterpart *A. breviligulata* remains unclear and poorly studied. Therefore, in this study we sought to understand the elements of competition between these dominant plant species. We conducted a greenhouse experiment in which two abiotic factors, burial and salt spray, were manipulated to compare the survival rates of *A. breviligulata* and *C. kobomugi* under competition. There are many abiotic elements that make survival in the foredune and primary dune environment challenging but substrate fluctuations and salt spray are the two most prominent and variable conditions, both historically and daily (Doody, 2012). Sand was added to gain a better understanding of burial tolerance; repeat burial of *C. kobomugi* has been demonstrated to cause mortality, whereas, species of *Ammophila* are well adapted to burial and may increase energetic shoot output (Wootton *et al.*, 2005; Yuan *et al.*, 1993). We hypothesized that: (1) *C. kobomugi* would be more successful than *A. breviligulata* in all competition treatments and (2) *C. kobomugi* would be more successful in monocultures than under competition conditions.

MATERIALS AND METHODS

Greenhouse setup: A competition study between *C. kobomugi* and native *A. breviligulata* was conducted in 2013 in the greenhouse of Villanova University, PA. Initial *A. breviligulata* n = 400 nursery grown “Cape” variety *A. breviligulata* seedling plugs, 5×5 cm in diameter and depth grown from duplicates sprouted spring 2013. *Carex kobomugi* is not commercially available in the US and *ex situ* facilitation of seeds germinate successfully 1/1000 seeds (Wootton *et al.*, 2003). Thus, 330 *C. kobomugi* were uprooted from the edge of a large CK-dominated stand at Island Beach State

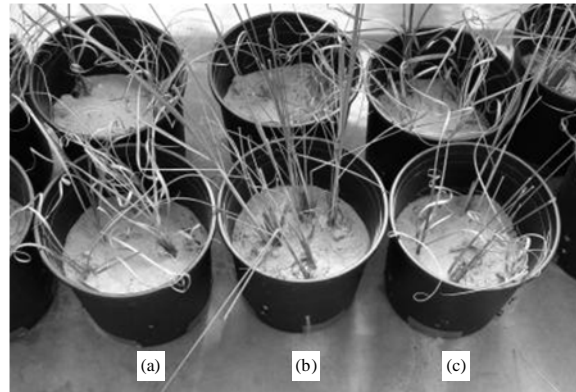


Fig. 1(a-c): Potted setup of the control monocultures of, (a) *C. kobomugi*, (b) *A. breviligulata* and (c) Competition polycultures

Park (IBSP), Ocean County, NJ (39°50'2.98"N, 74°5'18.34"W); these edge-plants should be the youngest and closest in age to *A. breviligulata* seedlings, making them comparable despite not being cultivated in a greenhouse.

The ramets were planted in storm washout sand four to a pot, in a monoculture or polyculture (Fig. 1). The pots were ≈ 1 kg plastic nursery containers with a ≈ 23 cm diameter and depth. To better mimic the drainage on dunes and prevent loss of sand, the pots were bottom-lined with plastic mesh, factory-cut drainage openings were reduced and 1.9 cm diameter holes were drilled, five on the bottom and two rows of six along the sides, into each pot. Each pot contained 15 cm of sand substrate and species were planted at the level they are found naturally: To the top of the crown for *A. breviligulata* and 2.5 cm below the collar for *C. kobomugi*. An initial subset of 330 *C. kobomugi* planted on September 6, 2013 died of anoxia from poor drainage in waterlogged sand. These were replaced on September 20, with new individuals harvested that day from IBSP; *A. breviligulata* ramets were not affected by the overly wet substrate and after resetting the experiment, N = 125 pots, 75 monoculture and 75 polycultures with 250 ramers per specie. The plants were given five weeks to acclimate before the onset of experimental treatments.

For the duration of study, the plants were maintained in conditions that mimicked summer temperature, light intensity and duration and rainfall to prevent the plants from entering arrested development of dormancy. Humidity was 70-80% at 26/18°C day/night under a regulated light intensity. When the natural brightness of the room dropped below $100 \mu\text{E m}^2 \text{sec}^{-1}$ 400 W overhead bulbs powered on to maintain summer-like day length. These lights in conjunction with maintaining the pots on the heated greenhouse floor, 21/18°C day/night, aided in drainage. The plants were watered based on IBSP's average weekly rain volume and frequency from June-August 2013: 33 mL of tap water 4 week.

Greenhouse experimental design: The treatment design was factorial with two experimental factors, salt and substrate amount. Two treatment levels per factor created four unique setups in a non-competitive (monoculture) or competitive (polyculture) background (Table 1). Substrate levels were a control, where no additional sand was added and high substrate where an additional 7.6 cm of sand was added, thus burying *A. breviligulata* to the ligule of the highest green leaf and almost completely covering *C. kobomugi* (Brown, 1997). Salt conditions consisted of unaltered controls

Table 1: Four unique treatment groups where each treatment has both a non-competitive (monoculture) or competitive (polyculture) background

		Factor 1: Substrate amount		×	Monoculture: No competition
		Control	Added sand		Polyculture: No competition
Factor 2: Salt spray	Control: No salt	Control	Burial		
	Salt spray	NaCl	Burial+NaCl		

receiving no salt and salt treatments in which pots were sprayed once daily with a NaCl solution at 3.5% salinity to mimic seawater. Plants were sprayed to coating but not enough to cause dripping (Oosting, 1945). The initial sample size was N = 125 pots, 75 monoculture and 75 polyculture, divided into one of the four treatments.

On October 27, 2013, after 5-weeks of acclimation, the original sample sizes had to be reassessed based on survival and living plants were cropped to standardized heights, 30 cm for *A. breviligulata* and 15 cm for *C. kobomugi*. The original N = 125 pots was reduced to 29 total pots (23%), 16 polycultures, divided into four pots per treatment and 13 monocultures, divided into 2-3 pots per treatment. Treatments were carried out for two months, November to mid-December with measurements taken on set days (Table 2); plant health was measured as a function of chlorophyll fluorescence, measured with an Opti-Sciences OS1-FL Modulated Chlorophyll fluorometer and growth, height of the tallest leaf crown to tip, as a proxy of mass. Individuals were considered dead if, the leaves were no longer green and cracked when bent.

Sem structural/morphological analysis: To initialize the infiltration process *C. kobomugi* and *A. breviligulata* leaves were cut in and directly set in glutaraldehyde *in situ* at IBSP on October 16, 2013. *Ex situ*, leaf sections were sliced with a clean razor blade and fixed in 2.5% (v/v) glutaraldehyde in 0.1 M PO₄ buffer (pH 7.0) for 24 h at 4°C. Sections were then washed thrice in 50 mM PO₄ buffer (pH 7.0) before being oxidized with 1% osmium tetroxide in 0.1 M PO₄ buffer (pH 7.0). Sections were then dehydrated in multiple acetone washes and critical point dried in a Leica® EM CPD300 critical point drier. Sections were mounted on planchets and sputter coated in on a 100-sec QT Timed Gold program of an EMS150R ES to prevent charging during imaging.

Samples were examined at 20 kv and 15 M to compare: (1) The density of bundle sheaths per leaf, (2) The density and structure of stomata and (3) Cuticle thickness. To quantify stomata an area was photographed at 200× (460×590 μm area) and all full and partial stomata were quantified. Similarly, the number of bundle sheaths was quantified by counting from a clean cross section of a whole leaf excision. The EDAX Genesis measurement tool was used to measure cuticle thicknesses in microns by zooming into an area where the cuticle was discernable at 1500× and measuring thickness at six different points spaced out along the leaf and averaged. We used JMP Pro 11.0 to analyze these data where all tests are two-tailed using an α = 0.05 as the threshold of significance and means presented as ± standard error.

RESULTS

Greenhouse experiment: Only 16 and 13% of the initial 250 per specie *A. breviligulata* and *C. kobomugi* ramets, respectfully, survived the 5 weeks acclimation period before the onset of experimental treatments (Table 3). Of those survivors, only 42% of the individuals remained alive for the total duration of the study. After beginning treatments, the first pot death occurred at day six and of the initial 29 pots, only 15 (52%) survived the full length of the study (Table 2). New tiller growth was only observed in 1-*C. kobomugi* and 7-*A. breviligulata* ramets and appeared

Table 2: Treatment sample sizes at each collection throughout the greenhouse experiment: October 30-December 20, 2013

		Julian date												
		3	3	3	3	3	3	3	3	3	3	3	3	3
		0	0	0	0	0	1	1	2	2	3	4	4	5
Type	Treatment group	3	4	5	6	8	0	5	2	6	3	0	8	4
Comp	Burial	3	3	3	3	3	3	3	2	2	2	2	2	2
Comp	Burial and salt	4	4	4	4	4	3	2	2	1	1	1	1	1
Comp	Control	4	4	4	4	4	4	4	4	4	4	4	4	4
Comp	Salt	4	4	4	4	4	4	4	4	4	4	4	4	4
CK-Mono	Burial	2	2	2	2	2	2	2	2	1	1	1	1	1
CK-Mono	Burial and salt	1	1	1	1	1	1	1	1	1	0	0	0	0
CK-Mono	Control	3	3	3	3	3	2	2	1	1	0	0	0	0
CK-Mono	Salt	2	2	2	2	2	2	2	2	2	2	2	2	2
AB-Mono	Burial	1	1	1	1	1	0	0	0	0	0	0	0	0
AB-Mono	Burial and salt	2	2	2	2	2	1	1	1	0	0	0	0	0
AB-Mono	Control	1	1	1	1	1	1	1	1	1	0	0	0	0
AB-Mono	Salt	2	2	2	2	2	2	2	2	2	2	2	2	1
Total N→		29	29	29	29	29	25	24	22	19	16	16	16	15

Table 3: Individual count of ramet survival after acclimation throughout the duration of the greenhouse experiment regardless of treatment: October 30-December 20, 2013

		Julian date												
		3	3	3	3	3	3	3	3	3	3	3	3	3
		0	0	0	0	0	1	1	2	2	3	4	4	5
Type	Group	3	4	5	6	8	0	5	2	6	3	0	8	4
Comp	<i>A. breviligulata</i> ramets	27	27	27	27	30	27	28	23	22	21	20	22	24
Comp	<i>C. kobomugi</i> ramets	18	18	18	19	18	15	15	12	10	8	8	8	7
Comp	Total Pots	15	15	15	15	15	14	13	12	11	11	11	11	11
Mono	<i>A. breviligulata</i> ramets	16	16	16	15	16	11	11	10	3	3	2	1	0
Mono	<i>C. kobomugi</i> ramets	15	14	14	14	14	13	13	11	11	6	5	5	0
Mono	Total <i>A. breviligulata</i> pots	6	6	6	6	6	4	4	4	3	2	2	2	0
Mono	Total <i>C. kobomugi</i> pots	8	8	8	8	8	7	7	6	5	3	3	3	0

during week two of the study: three *A. breviligulata* monocultures receiving salt spray and four competition pots-two burial+salt, one salt spray and one burial treatment grew a new stem and the one *C. kobomugi* that produced a new stem was in a monoculture control pot, no salt or burial.

Because of the small and uneven sample sizes within groups, no statistical inferences were made, as they would have little to no power for interpretation. However, detailed observations were made throughout the study. Anecdotally, both species invested more energy towards the growth of 1-2 leaves, as opposed to all leaves as one leaf was always noticeably taller than the others. The *C. kobomugi* individuals each had at least one dead leaf throughout and this was especially true in treatments receiving salt spray. The *A. breviligulata* individuals under stress curled leaves laterally into a tight straw-like shape, protecting the adaxial leaf surfaces. Conversely, *C. kobomugi* individuals curled leaves vertically in a variable corkscrew shape. Not all leaves of a ramet corkscrewed, none did so uniformly and corkscrewed leaves were visibly dehydrated compared to others (Fig. 2).

Microscopy: *Carex kobomugi* proved more rugged than anticipated as 6 h in Osmium was not enough to fully infiltrate and kill the tissue. *Carex kobomugi* samples had to be soaked in Osmium overnight (12+h) to fully infiltrate. Similarly, despite ample infiltration, after being place in resin, *C. kobomugi* samples still floated. *Carex kobomugi* has a thicker cuticle than *A. breviligulata*: $\bar{x}_{AB} = -3.20 \pm 0.19 \mu\text{m}$ n = 7; $\bar{x}_{CK} = 3.82 \pm 0.12 \mu\text{m}$ n 10; $t_{11.05} = 2.75$, p = 0.02) Fig. 3. Stomata location and potentially density were different. Interestingly, stomata are on the adaxial leaf surface of *A. breviligulata* and their density could not be quantified because they are pitted in folds among

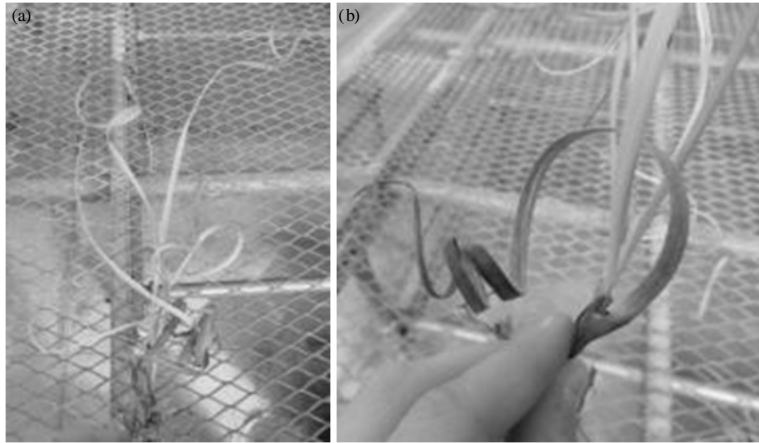


Fig. 2(a-b): Examples of corkscrewed *C. kobomugi* individuals in the greenhouse from October 30-December 20, 2013

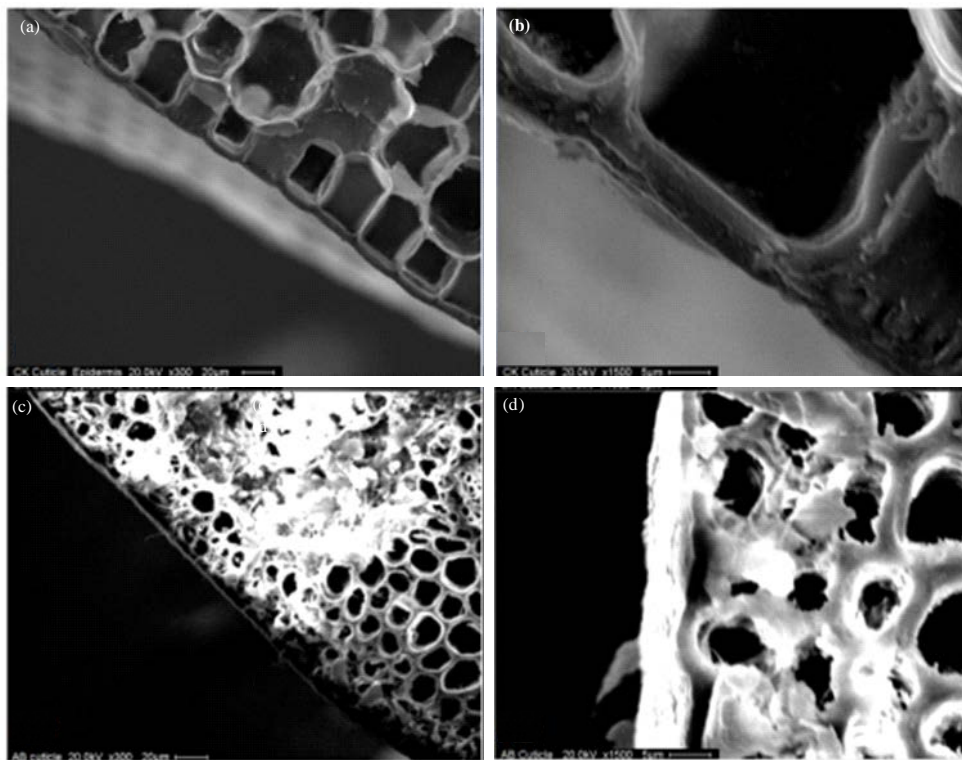


Fig. 3(a-d): SEM of (a, b) *C. kobomugi* and (c, d) *A. breviligulata* cuticles magnified to 300 and 1500x

dense trichomes; conversely, *C. kobomugi* stomata are on the abaxial leaf surface, with no pitting, trichomes, or folds and with a mean density of 70 stomata ($n = 10$) at 200 \times (Fig. 4). *Carex kobomugi* was more vascularized with more bundle sheaths than *A. breviligulata* ($\bar{x}_{AB} = -19.63 \pm 1.28$ $n = 8$; $\bar{x}_{CK} = 33.40 \pm 1.71$ $n = 10$; $t_{2,13} = 6.45$, $p < 0.0001$) (Fig. 5). The *A. breviligulata* abaxial and *C. kobomugi* adaxial leaf surface lacked distinguishable features.

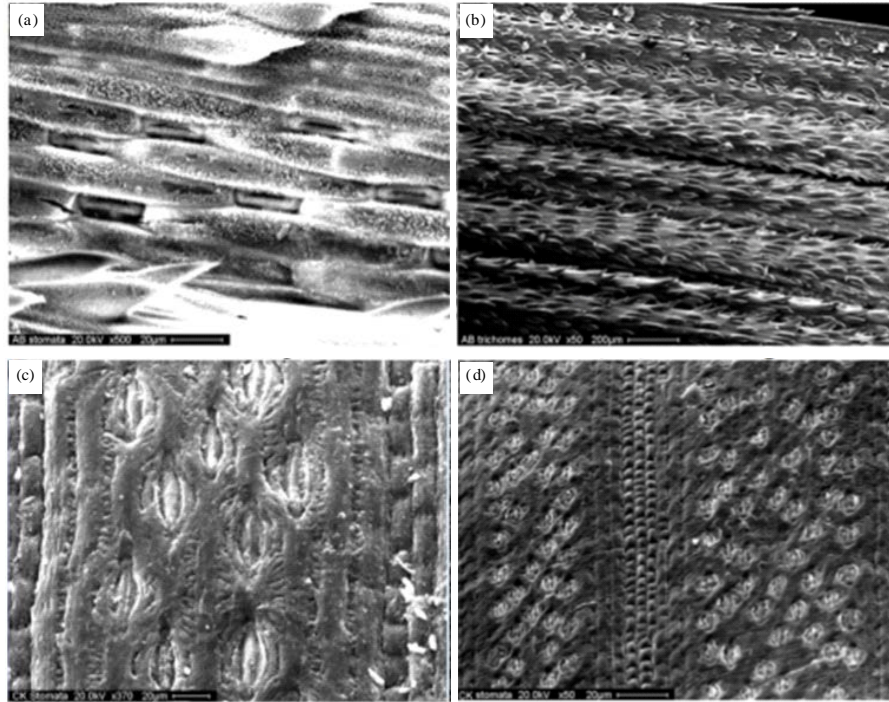


Fig. 4(a-d): At 500x magnification, (a) *A. breviligulata* pitted stomata can be discerned within folds (b) Among trichomes at 50x magnification and (c, d) *C. kobomugi* abaxial leaf surface houses non-pitted stomata in large densities c and d

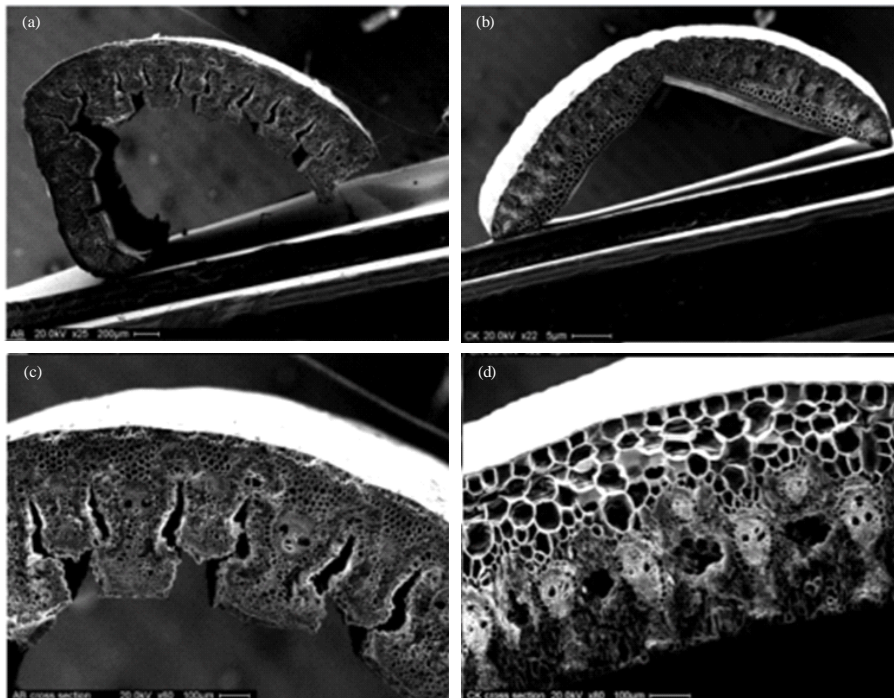


Fig. 5(a-f): Continue

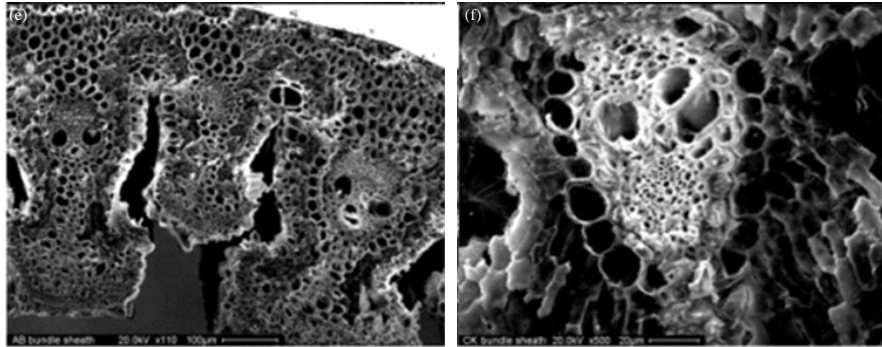


Fig. 5(a-f): Vascularization of the plants, at different magnifications: *A. breviligulata* (left) and *C. kobomugi* (right). Note the curling and folds of *A. breviligulata* where, each fold has a bundle sheath at its center. *C. kobomugi* bundle sheaths are distributed in a zigzag to straight pattern throughout the width of the leaf

DISCUSSION

The morphology of the species was very disparate and support differing water use efficiencies. The structural organization of larger and smaller vascular bundles on folds is an adaptation of *A. breviligulata* for adaxial leaf folding to prevent water loss (Emery *et al.*, 2010). Conversely, *C. kobomugi* blades do not fold which may make the species more structurally rigid but less adapted to combat evaporative water loss (Yura and Ogura, 2006); the thicker observed cuticle of *C. kobomugi* may counteract this but this result may be skewed and subjective as it was not possible to attain the same clarity for all samples with SEM that would be possible with TEM. Stomatal abundance only on the adaxial leaf surface may be another adaptation of *A. breviligulata* as many species of the Poaceae family have stomata on both surfaces (Zarinkamar, 2006). Conversely, Cyperaceae have linearly arranged stomata on the abaxial surface but *C. kobomugi* may have a greater stomatal density than other sedges; the highest stomata frequency observed by Zarinkamar (2006) was 179 mm^{-2} in *C. nigra* and here *C. kobomugi* averaged 259 mm^{-2} . More in depth physiological analyses are necessary to understand the adaptive strengths and weaknesses of the two species in various biotic and abiotic conditions.

Carex kobomugi did not transport well. The initial September 6 subset died due to anoxia, as the pots were not draining through the water column as they would naturally atop developed dunes. *A. breviligulata* was unaffected by excessive sand moisture despite being characterized as a species that does not tolerate soil moisture (USDA., 2014a). Conversely, *C. kobomugi* suffered high mortality of nearly 100% though classified as preferring moist to wet soils by commercial dealers and uncharacterized by the USDA (2014b). The literature may be incorrect and *A. breviligulata* may better adapted to wet substrate than supposed; water logged conditions cause a buildup of toxic byproducts from anaerobic respiration, which can inhibit root functioning resulting in leaf dehydration (Sinclair and Lyon, 2005) but the morphology - pitted and trichome protected stomata and adaxial folding of *A. breviligulata* may better prevent water loss than *C. kobomugi*.

Despite proper drainage, general survival of both species in the second September 20 subset through acclimation and the testing duration was still very low and is therefore, likely a function of other negative factors; we attribute the general low survival to a lack of nutrient availability and a potential lack of mycorrhizae. We did not supplement the substrate with any nutrient inputs

because nutrient availability on the dunes at IBSP was very low and homogenous (Reo unpublished data). However, rainfall inputs may play a major role in supplying coastal areas with nitrogen and other essential atmospheric nutrients (Valigura *et al.*, 1996; Kocak *et al.*, 2010) that quickly drain through the water column. Similarly, establishment may be contingent on existing fungal spores in soils (Gemma and Koske, 1988; Sylvia and Will, 1988) which may not have been present but was not tested for the roots of the *A. breviligulata* plugs may be mycorrhizal as planting stocks from certain locations are inherently mycorrhizal as a result of the greenhouse growing protocols used (Gemma and Koske, 1997).

Low survival of *C. kobomugi* may also be a function of transplant shock and related stress associated with physical uprooting. Loss of belowground mass from physical uprooting was inevitable given the fine and stringy structure of the rhizomes and roots. Losing root mass and root exposure to ambient air and heat during transport could have put the plants into an initial state of shock or a state of arrested growth and development (Tuteja, 2007) from which they never recovered. Testing of the chemical composition of individuals with regards to heat shock proteins (Vierling, 1991) and abscisic acid (Tuteja, 2007) assays would be reliable ways to test this but are out of the scope of this study. Similarly, transplanting individual rhizomatous clonal ramets from genets could reduce survival. Once established, *C. kobomugi* stands are virulent and extremely difficult to eradicate (Ishikawa and Kachi, 1998; Woodward and Quinn, 2011; Wootton *et al.*, 2003) but as individuals, they do not appear as robust. A lack of resource sharing among neighboring conspecifics may decrease survivorship, as has been shown in seaside goldenrod (*Salidago sempevirens*) (Donohue, 2003). The commercially grown *A. breviligulata* plugs likely had the 'advantage' of being healthier at the onset of the experiment but field harvested ramets would likely respond with similarly low survivorship from high initial stress. Understanding why *C. kobomugi* dominates *en situ* and has low survivorship *ex situ* has implications for preventing establishment and directing management plans.

Time of year to transplant, may also explain the low survival rates. Many trees and grasses do well planted in the spring whereas others do better planted in the fall such that transplant time can be critical for successful establishment (Richardson-Calfee and Harris, 2005; Page and Bork, 2005). Therefore, a spring planting of *C. kobomugi* has potential to yield higher survival rates but some herbaceous plants (Fattorini, 2001) and grass species simply do not transport well regardless of the season (Glenn *et al.*, 2001; Kering *et al.*, 2012). Given this and low *C. kobomugi* seeding survival rate (Wootton *et al.*, 2003), we did not feel replication would yield different results. Monitoring already established stands *in situ* may produce more meaningful results than greenhouse analyses.

Both species appeared to behave similarly regarding energy allocation but differ in their response to stress. In polycultures, growth was observed in 1-2 leaves as opposed to all as with the monocultures and could thus be a competitive response. The species respond differently to stress: *A. breviligulata* protect the stomata on their adaxial surface by curling whereas, *C. kobomugi* leaves corkscrew. Corkscrewing was observed most predominantly in the presence of salt and could be a function of allocation of Na to older leaves, which a visually apparent evolutionary strategy of some mangrove species (Cram *et al.*, 2002) the evolutionary significance of this action in *C. kobomugi* is unknown and requires further attention.

The questions raised in this study should be used to begin filling in the gaps in our understanding of the life histories of dominant coastal flora. These life histories underpin coastal

stabilization and erosion prevention. Information is likely the key to understanding how to contain *C. kobomugi* and thereby maintain the natural aesthetic and functioning of Mid-Atlantic coastal dune habitats dominated by *A. breviligulata*.

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