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Joseph L. Kowalski

The University of Texas Rio Grande Valley

Hudson R. DeYoe

The University of Texas Rio Grande Valley

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Recommended Citation

Kowalski, Joseph L. and DeYoe, Hudson R.. "Flowering and seed production in the subtropical seagrass, *Halodule wrightii* (shoal grass)" *Botanica Marina*, vol. 59, no. 2-3, 2016, pp. 193-199. <https://doi.org/10.1515/bot-2015-0099>

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Short communication

Joseph L. Kowalski* and Hudson R. DeYoe

Flowering and seed production in the subtropical seagrass, *Halodule wrightii* (shoal grass)

DOI 10.1515/bot-2015-0099

Received 26 November, 2015; accepted 14 April, 2016; online first 25 May, 2016

Abstract: Reproductive structures of the seagrass, *Halodule wrightii* Ascherson (shoal grass) are cryptic and ephemeral, but were found on several occasions at several sites over more than a decade in the subtropical Laguna Madre (USA). Structures align with descriptions for *H. wrightii*. Male, but no female flowers were found, but the numerous fruit-bearing shoots imply the occurrence of pistillate flowers. Mean seed bank density was 890 seeds m⁻² (1900–5200 m⁻²). Sexual reproduction in *H. wrightii* is more common than previously believed and the seed bank reserve may contribute to its ecological role as a colonizer of disturbed sediments.

Keywords: flowers; *Halodule wrightii*; reproductive ecology; seed bank.

Seagrasses grow and expand by clonal expansion, establishment of vegetative fragments, and sexual reproduction (Hall et al. 2006). Of these mechanisms, sexual reproduction is critical to maintain the genetic diversity of populations (Reusch et al. 2005). The presence of flowers and seeds is also important in the taxonomic description of a species (Phillips 1960). Seeds of some ruderal seagrass species can also play a key role in revegetation of disturbed seagrass beds (Rasheed 2004). Three quarters (ca. 500 km²) of the sea bed of the subtropical lagoon, Laguna Madre (LM) of Texas has historically been vegetated (Onuf 2007), but an extensive freshet in 2010 resulted in decreased areal cover in most seagrass species (DeYoe

and Kowalski 2014). *Halodule wrightii* Ascherson (shoal grass) did not experience overall decline and remains an abundant and ecologically important seagrass that often grows in disturbed sediments (Pulich 1982). Reproductive structures of *H. wrightii* have been found from Brazil, several localities along the Gulf of Mexico and Caribbean Sea and the east coast of North America (Table 1). Like most seagrass species, the flowers of *H. wrightii* are dioecious (Moffler and Durako 1987). The broad geographical range in which *H. wrightii* flowers and sets fruit suggests that sexual reproduction of *H. wrightii* is more common and cosmopolitan than the literature indicates, but the cryptic and ephemeral nature of these structures hinders documentation. The purpose of this investigation was to describe the occurrence, abundance, and selected areal extent of sexually reproductive material of *H. wrightii* in the LM, to compare and update these observations with literature accounts, and to address its taxonomic standing.

We found flowering shoots, fruits, and seeds of the seagrass *H. wrightii* in LM during late spring and summer of 1995, 1996, 2007, 2008, and 2009 at three locations. Prior to these observations, *Thalassia testudinum* Banks ex König (turtle grass) and *Syringodium filiforme* Kützing (manatee grass) were the only seagrass species documented to have produced flowers and fruit in the LM (Kaldy and Dunton 1999). We define “fruits” as pollinated pistillate flowers attached to the parent shoot irrespective of stage of development, and “seeds” as detached from the parent shoot. Sediment seed reserve is defined here as potential reproductive units, irrespective of viability.

Discovery of *H. wrightii* seeds was initially made serendipitously as part of a study of leaf production techniques for *H. wrightii* (Kowalski et al. 2001) performed between 1995 and 1997. Reproductive shoots and seeds were found in cores (9-cm diameter, 10-cm deep) taken for biomass and shoot production determinations (Kowalski et al. 2001). Flowers, fruits, and seeds were found from June 1995 through September 1995 and from June 1996 through August 1996 at LM107 (Table 2) on nine sampling dates. Over the first four sampling dates in 1995, 24 cores were collected. Eight cores were collected from

*Corresponding author: Joseph L. Kowalski, Center for Subtropical Studies and Department of Biology, The University of Texas Rio Grande Valley, 1201 West University Drive, Edinburg, TX 78539, USA, e-mail: joseph.kowalski01@utrgv.edu

Hudson R. DeYoe: Center for Subtropical Studies and Department of Biology, The University of Texas Rio Grande Valley, 1201 West University Drive, Edinburg, TX 78539, USA

Table 1: Record of previous occurrences of flowers, fruits, and seeds in *Halodule wrightii* from different localities.

Locality	Reproductive structure(s)	Comments	Timing/Season	Source
Texas, USA (Redfish Bay)	Flowers (male and female), fruit	Fruit maturation in laboratory culture	Apr	McMillan (1976)
Texas, USA (Redfish Bay and Port Mansfield, Lower Laguna Madre)	Seeds	Seeds sieved from sediment (seed bank estimates)	No data	McMillan (1981)
St. Croix, US Virgin Islands (Jacks Bay)	Seeds	Seeds sieved from sediment (seed bank estimates)	No data	Johnson and Williams (1982)
St. Croix, US Virgin Islands (Jacks Bay)	Flowers (male and female), fruit	Early Apr maximum staminate production	Mar-early May	Oliveira et al. (1983)
Brazilian coast (several localities)	Flowers (male and female), fruit	Maximum fruit production in mid-Apr	No data	McMillan (1985)
Texas, USA (Upper and Lower Laguna Madre)	Seeds	Taxonomic/descriptive	No data	Eleuterius (1987)
Alabama, Louisiana, Mississippi and Chandeleur Sounds)	Flowers (male and female?)	Seeds sieved from sediment (seed bank estimates)	Late May-June	Ferguson et al. (1993)
North Carolina (Pamlico, Bogue, Roanoke, and Core Sounds)	Flowers (male and female), fruit, seeds	65% of flowers staminate	May-Aug (flowers)	McGovern and Blankenhorn (2007)
Mississippi Sound (Alabama)	Fruit	Salinity 12-34	Late June-Sept	This study
Texas, USA (Lower Laguna Madre - LLM107) (26° 09' N, 97° 14' W)	One male flower, fruit, and seeds	-	June-Sept	This study
Site ABC: Approximately 5 km north of the Brazos-Santiago Pass, west of Andy Bowie Park (26° 08' N, 97° 10' W)	Fruit	See Kowalski et al. (2009) for site description	June-July	This study
Site IB (Isla Blanca Park, South Padre Island, Texas): Approximately 1 km north of the Brazos-Santiago Pass (26° 04' N, 97° 09' W)	Thirteen male flowers and fruit	50-70 cm water depth	June-July	This study
		50-70 cm water depth	June-July	This study

Table 2: Number of flower-bearing and fruit-bearing shoots, individual detached seeds, and percentage of sexually reproductive shoots sampled from 9-cm diameter (0.006 m²) cores for *Halodule wrightii* from LLM107 (1995–1996), and hand-scooped sediment samples from sites ABC and IB (see Table 1 for details and locations) from 2007 to 2009, Lower Laguna Madre, Texas.

Sample date	% cores w/ flowers or fruits	Flower-bearing shoots (per core)	Fruit-bearing shoots (per core)	Detached seeds (per core)	% Sexually reproductive shoots	Sediment seed reserve (m ⁻²)
24-June-95 ^a	38	0	16	25	4.23	4064
7-July-95 ^a	4	0	2	3	8.70	487
18-July-95 ^a	42	0	18	32	4.99	5201
5-Aug-95 ^a	28	0	3	3	3.75	487
19-Aug-95 ^a	4	0	1	0	2.78	0
2-Sep-95 ^b	0	0	0	7	0.00	1138
29-Sep-95 ^b	0	0	0	2	0.00	325
4-May-96 ^b	0	0	0	0	0.00	0
15-June-96 ^b	38	0	8	9	6.11	1463
27-July-96 ^b	62	0	9	12	4.05	1950
24-Aug-96 ^b	12	1	1	0	3.30	0
23-June-07 ^c	NA	0	NA	6	NA	NA
28-June-08 ^c	NA	0	NA	7	NA	NA
13-Apr-09 ^c	NA	13	NA	NA	NA	NA

Percentage of sexually reproductive shoots based on the ratio of flower and fruit-bearing shoots to total shoot count per core.

^a24 cores collected per sampling date.

^bEight cores collected per sampling date.

^cNot based on cores (haphazard scoops of sediment).

the site on all subsequent trips (Kowalski et al. 2001). Reproductive structures on shoots were noted during processing and enumerated. Length and width of staminate flowers and length and diameter of fruits and seeds were measured to the nearest 0.1 mm using a caliper. Fruits were typically found in pairs attached to maternal shoots. Fifteen fruits were measured. Thereafter, individual *H. wrightii* seeds were counted from each core, but not measured.

A decade later, seeds, but no flowers or fruits, were collected during June 2007 and June 2008 at two sites (IB, ABC) on the east side of the LM (Tables 1 and 2). Thirteen staminate flowers were collected at the IB site in April 2009. Sampling was haphazard by collecting scoops of sediment with intact *H. wrightii* leaves, shoots, rhizomes and roots which were then examined in the field for the presence of sexual reproductive structures. Fruits were rinsed of sediment and stored in plastic bags on ice to later record flower and seed dimension and color. Water column temperature (°C; bulb thermometer) and salinity (refractometer) were recorded during each survey. Flowers from the 2009 survey were preserved in FAA (1 unit formaldehyde, 5 units of ethylic alcohol, 0.5 unit of glacial acetic acid and 3.5 units of distilled water). Voucher specimens of *H. wrightii*, flowers, shoots bearing flowers, and fruits were deposited in the herbarium of the University of Texas Rio Grande Valley, Edinburg, Texas.

Water temperature at all sites (all surveys) ranged from 22 to 24°C during the flowering period (late April and May)

and from 28° to 31°C during seed production (June to September) while salinity varied from 32 to 40. The production of flowers and fruits in tropical and subtropical seagrasses, including *H. wrightii*, has been correlated with water temperature and, to a lesser degree, photoperiod and occurs during specific times of the year (McMillan 1976, 1982). A total of 72 flower- and fruit-bearing shoots were collected (Table 2). Among these, 14 staminate flowers and no pistillate flowers were found, although the presence of fruits and seeds indicates that female flowers must have been present and there are no accounts of apomixis occurring in *H. wrightii*. Mean number of reproductive shoots for *H. wrightii* (mean±SE) was 3.4%±0.9 and ranged from 0 to 8.7%, well below the ranges of 7.9–19.8% in *Posidonia oceanica* (Ballesi and Cinelli 2003) and 13–30% in *T. testudinum* (Kaldy and Dunton 1999), but similar to the ruderal species, *Halophila decipiens* (4%; Hammerstrom et al. 2006). Staminate flowers were reported by Cox and Knox (1989) as rarely longer than 5 mm and positioned on a stalk from the leaf sheath above the sediment to release filiform pollen. Mean anther length was 3.5 mm and ranged from 3.0 to 5.7 mm (Figure 1), within the range described by Moffler and Durako (1987), Phillips and Meñez (1988), and Ferguson et al. (1993) for *H. wrightii*. Mean anther width was 0.8 mm.

Mean fruit size from LM107 was 2.2±0.1 mm in diameter and 2.6±0.1 mm long (Figure 1) and ranged in color from olive to tan, similar to other descriptions for *H. wrightii* (Phillips et al. 1974, Ferguson et al. 1993,

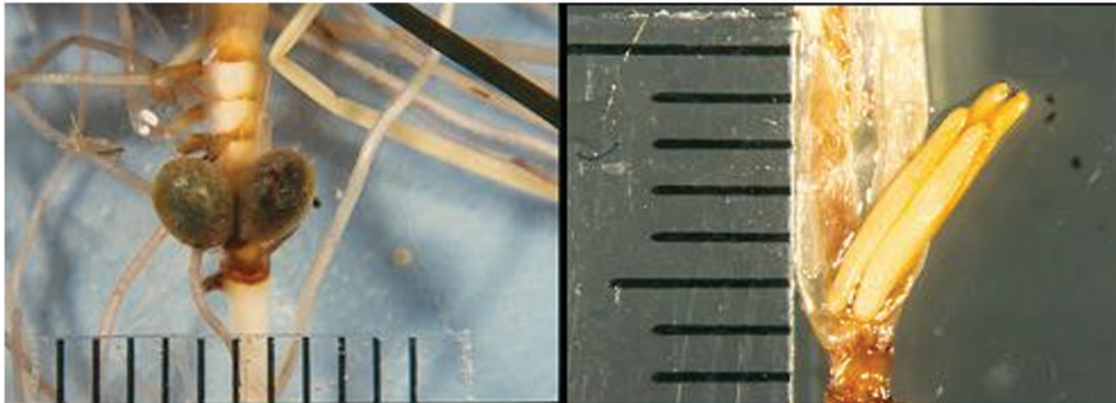


Figure 1: Two *Halodule wrightii* fruits attached to the maternal shoot (left) and staminate flower of *H. wrightii* (right) from the Laguna Madre, Texas. Scale in mm for both images.

McGovern and Blankenhorn 2007). *Halodule wrightii* in the LM produced fruits from late June through September, as also noted by McGovern and Blankenhorn (2007) for Mississippi Sound, Alabama. Shoot density at site LM107 varied between 5300 and 6100 shoots m^{-2} (Kowalski et al. 2001). Of the detached seeds collected in June 2007, five were a light cream/tan in color and one was black. Seven seeds were found in June 2008. Six were olive and one tan in color. Mean seed diameter was 4.8 ± 0.1 mm in 2007 and 2.6 ± 0.1 mm in 2008. Since fruits and seeds were found as early as June, anthesis must occur in May and possibly as early as April (Table 2). All of the staminate flowers collected in 2009 (Site IB) were still enclosed in the bundle sheath (not emerged) suggesting that anthesis occurs as early as April. Flowering in *H. wrightii* starts as early as March in the Virgin Islands (Johnson and Williams 1982) and in late May in the northern Gulf of Mexico (Eleuterius 1987). Shoot density at these eastern LM sites ranged from 8209 ± 685 shoots m^{-2} in May 2007 to 9185 ± 1065 shoots m^{-2} in May 2008. These shoot densities are typical for *H. wrightii* in the LM (Kowalski et al. 2001, Kaldy et al. 2004, Kowalski et al. 2009).

The importance of sexual reproduction in *H. wrightii* has not been well appreciated. Studies suggest that genetic structure in most seagrass species is more diverse than can be explained by purely clonal growth (Angel 2002, Larkin et al. 2010). The implication is that successful sexual reproduction and seed dispersal must be occurring at a greater rate than has been observed (Kenworthy 1999, McMahon et al. 2014). Rasheed (2004) suggested that seed output by *Zostera marina* may compensate for slow rhizome growth and facilitate colonization of denuded areas. The contribution of a seed bank to *Z. marina* revegetation along the east coast of North America can be significant in restoration efforts when water quality is suitable

for seedling growth (Jarvis and Moore 2010). The presence of flower and fruit-producing shoots of *H. wrightii* in the LM, coupled with the abundant seed bank (Table 2), indicates that flowering and seed dispersal play a significant role in the establishment and maintenance of *H. wrightii* populations in the LM. Seed dispersal in *Posidonia australis* (Australia) and *Thalassia testudinum* (USA) occurs with fruit floating several kilometres before sinking (Kaldy and Dunton 1999, McMahon et al. 2014, Ruiz-Montoya et al. 2015). Seeds of *H. wrightii* are negatively buoyant and typically remain in place. The Redhead duck (*Aythya americana*) winters in the LM and consumes the rhizome/root organs of *H. wrightii* (Woodin 1996) and offers an alternative way to carry fruits and/or seeds to new locations.

Detached seeds of *H. wrightii* have been previously found in LM sediments (Table 1). McMillan (1983) estimated *H. wrightii* sediment seed reserve, seed longevity, and germination for sites from Redfish Bay, near Corpus Christi, Texas (USA) and the Upper Laguna Madre, Texas. In this study, vegetative and sexual reproductive material of *H. wrightii* conformed to the descriptions of den Hartog (1970) and Phillips and Meñez (1988).

Flowering and fruit production appeared to occur in patches within *H. wrightii* beds in the LM. During a *H. wrightii* leaf production study (Kowalski et al. 2001), clumped dispersion of flowers/fruits in *H. wrightii* was noted based on the low percentage of cores that contained flowers/fruits (Table 2). Clumped dispersion of flowering and fruit production has been postulated as a consequence of the dioecious and clonal nature of seagrasses (den Hartog 1970, Campey et al. 2002, Balestri and Lardicci 2008).

The description of sexual reproductive structures is important for taxonomic purposes. This is noteworthy in the case of *H. wrightii* whose taxonomic status has been debated. Two *Halodule* species, *H. wrightii* and

H. beaudettei, have been described for the Gulf of Mexico and Caribbean Sea based exclusively on differences in vegetative (leaf tip morphology), but not sexual, characteristics (den Hartog 1970). Phillips et al. (1974) examined *H. wrightii* from the mid-Texas coast, described the flowers and concluded that *Halodule* in their collections was *H. wrightii*. They discounted the taxonomic value of vegetative characters (leaf tip morphology) for species discrimination in *Halodule* (Phillips et al. 1974) since the leaf tip features used to discriminate between the two species by den Hartog (1970) were found within the same meadow. We also found leaf tip morphology to vary in plants in the same meadow (IB site) where staminate flowers were found, as similarly reported by Phillips et al. (1974). The floral and fruit descriptions presented here align with those described for *H. wrightii* by den Hartog (1970) and Phillips et al. (1974). As there are no descriptions of flowers or fruit structures of for *H. beaudettei* by den Hartog (1970), we concur with the findings of Phillips et al. (1974). Clearly, an in-depth analysis of the *Halodule* genus at a global scale is necessary that includes molecular tools.

Sexual reproduction in *H. wrightii* has been reported as uncommon and poorly understood, probably because its small, cryptic flowers are inconspicuous and are ephemeral. Thus, sexual reproductive structures may have been overlooked. These observations, which have occurred over more than a decade, provide a better understanding and description of the timing of sexually reproductive events and can contribute to our understanding of phenological aspects of *H. wrightii* in the LM. Knowledge of *H. wrightii* phenology is important locally since *H. wrightii* comprises roughly 300 km² of the seagrass coverage in the LM (Onuf 2007) and *H. wrightii* is the species of choice in replanting efforts, especially in the Gulf of Mexico (Fonseca et al. 1996, Hammerstrom et al. 1998, Sheridan et al. 1998) where it stabilizes sediment and serves as shelter for commercially and recreationally important animals (Pulich 1982).

A related, but equally important aspect of sexual reproduction in seagrasses is the use of seeds in the re-establishment of disturbed or destroyed meadows (Orth et al. 1994). van Tussenbroek (personal communication) found that *H. wrightii* re-established itself by seeds after almost total extirpation following hurricane Wilma (2005). Finally, seed production in some seagrass species, such as *Zostera marina* L., can be an important food source for animals, such as crabs (Luckenbach and Orth 1999, Orth et al. 2007). It is unknown whether the seeds of *H. wrightii* are utilized by animals other than the Redhead duck, but our understanding of how animal vectors play a

role in seagrass dispersal is improving through the study of movement ecology (McMahon et al. 2014).

The *H. wrightii* seed bank found at LM107 was 1890 seeds m⁻² (SE=638 seeds m⁻²) which is at the higher end of the range reported by McMillan (1981), who documented a seed bank range of 26–3120 seeds m⁻² (mean=260 seeds m⁻²) at the north end of the LM. A seed bank provides an opportunity for rapid re-vegetation, compared to vegetative expansion (Orth et al. 1994, Sumoski and Orth 2012) as seeds do not need to be imported. Perhaps transplanting sediment containing *H. wrightii* seeds could be a viable and economical means to re-vegetate impacted sites. Orth et al. (2006) made a comparison of buoyancy potential, seed bank size (density), dormancy (persistence), and seedling survival. *Halodule* spp. seeds are all negatively buoyant, and the species had among the highest seed bank density (ca. 20,000 m⁻²) and longest dormancy, but was among the lowest for seedling survival (<2%) across 11 cosmopolitan seagrass species. It may well be that *Halodule* spp. employs a trade-off between low survival rates offset by a large seed bank size to ensure survival.

Acknowledgments: We thank L.H. Hirsch for sample processing and thanks to Don Hockaday of The University of Texas Rio Grande Valley Coastal Studies Laboratory for his assistance and the use of the lab and equipment. We are grateful for critical review and discussion of an earlier version of the manuscript by Tim Glasby, Brigit van Tussenbroek, Jud Kenworthy, and to Patrick Larkin for comments on an early version. We thank two anonymous reviewers for improvement of the original manuscript. This research was funded by The Texas Higher Education Coordinating Board (Advanced Research Program Grant #003658-419) and a grant from The University of Texas-Pan American Faculty Research Council. This is publication number CSS 2016-02 of the UTRGV Center for Subtropical Studies.

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Bionotes



Joseph L. Kowalski

Center for Subtropical Studies and Department of Biology, The University of Texas Rio Grande Valley, 1201 West University Drive, Edinburg, TX 78539, USA
joseph.kowalski01@utrgv.edu

Joseph L. Kowalski is a research associate at the University of Texas Rio Grande Valley in Edinburg, Texas. He has studied the ecology and physiology of seagrasses and macroalgae for more than 20 years. Current research focuses on the impact of hyposalinity on the metabolism of seagrasses.



Hudson R. DeYoe

Center for Subtropical Studies and Department of Biology, The University of Texas Rio Grande Valley, 1201 West University Drive, Edinburg, TX 78539, USA

Hudson R. DeYoe is a Professor at the University of Texas Rio Grande Valley in south Texas. His expertise is in aquatic ecology with a focus on algal and seagrass ecology and human impact on aquatic systems.