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Seasonal Growth, Biomass Allocation, and Invasive Attributes Manifested by *Dioscorea bulbifera* L. (Air-Potato) Plants Generated from Bulbils in Florida

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Dioscorea bulbifera is a serious invader of various ecosystems in Florida, where plants generated by its two morphotypes climb aggressively and smother supporting vegetation. There is a dearth of published research on its invasive biological attributes including vine growth and biomass production by plants generated from bulbils. Herein, we assessed these parameters in common garden studies by planting bulbils from four biomass categories (PBBCs I–IV) of both morphotypes. Vine lengths, longevity-based growth rates (VLGR), biomass, and quantities of leaves and daughter bulbils in both morphotypes showed positive correlation with the biomass of planted parental bulbils. This indicated similarity between corresponding attributes in two morphotypes. Total vine length showed strong positive correlation with VLGR, biomass, and quantities of leaves and bulbils. Overall vine longevity among plants from PBBCs I–IV did not significantly differ whereas the total vine lengths, VLGRs, number of branches, and quantities of leaves and bulbils increased with the biomass of the parental bulbils. Plants recruited by smaller bulbils allocated more biomass to leaves and tubers compared to stems and bulbils, whereas the plants recruited by larger bulbils allocated more biomass to leaves and bulbils compared to tubers and stems. Higher proportion of biomass allocation to leaves and bulbils presumably ensures immediate faster growth, longer vines, and a greater number of daughter bulbils for future recruitment of new plants. Vine length (associated with faster growth rate, capable of blanketing supporting structures and producing large quantities of bulbils) has been noted as the primary invasive biological attribute that facilitates *D. bulbifera*'s status as a noxious exotic weed in Florida. Control measure that can reduce vine length should reduce or eliminate the invasive behavior of *D. bulbifera* in Florida.

Nomenclature: Air-potato, *Dioscorea bulbifera* L.

Keywords: Biomass production, common garden study, growth rate, invasive attributes, morphotypes, tuber.

Dioscorea bulbifera L. (air-potato, also known as air yam or aerial yam), native to Asia and Africa (Burkill 1960; Tindall 1993), has become one of the most troublesome Category 1 noxious invasive weeds in Florida by invading multiple types of habitats, including tropical hammocks and urban ecosystems (FLEPPC 2009; Gordon 1998; Hammer 1998; Pemberton and Witkus 2010; Shultz 1993). Reportedly, it was first introduced in Florida in 1905 (Coursey 1967; Morton 1976; Nehrling 1933, 1944) and now it has spread and naturalized in Alabama, Georgia, Hawaii, Louisiana, Mexico, Mississippi, Puerto Rico, Texas, West Indies, and central and northern South America (Nesom and Brown 1998; USDA-SCS 1982; Wheeler et al. 2007). *Dioscorea bulbifera* vines invade multiple types of habitats in Florida (Schultz 1993) and vigorously exploit disturbed sites, such as hurricane-

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Management Implications

The exotic invasive air potato vine *D. bulbifera* has become a serious problem for public and private land managers across Florida and beyond by blanketing and smothering native vegetation. Despite its common occurrence in Florida, there are no published research data related to the role of propagule biomass on the resulting vines' growth rate, biomass, and invasive biological traits. We conducted common garden studies using vegetative propagules (parent bulbils) ranging from small to large biomass and examined the growth and biomass of the plants generated from these bulbils. Biomass of the parent bulbils of both morphotypes was positively correlated with total vine lengths, growth rates, and the number of branches, leaves, and bulbils. The vine longevity of plants generated by bulbils of all sizes was not significantly different. However, the total vine length, vine growth rates, and the number of branches, leaves, and bulbils increased with the biomass of the parent bulbils. Plants recruited by smaller bulbils allocated a major proportion of total biomass to leaves and tubers compared to the stems and bulbils, whereas the larger bulbils allocated a greater proportion of total biomass to bulbils and leaves compared to tubers and stems. Total vine length was positively correlated with the total plant biomass. Reduced vine length should have concomitant negative impacts on leaf and bulbil production. These reductions should, in turn, negatively affect (1) plant biomass and the number of branches and leaves that are responsible for causing smothering effects on invaded plant communities and (2) bulbil production that will have direct negative impact on plant recruitment and invasion of the new areas. Therefore, control measures that reduce seasonal vine length should reduce the quantity of bulbils and hence invasiveness of *D. bulbifera* vines in Florida.

damaged forest canopies, thereby interfering with the recovery of native vegetation (Gordon et al.1999; Horvitz et al. 1998; Horvitz and Koop 2001). More recently, *D. bulbifera* has been described as a transformer species in Florida's environment capable of altering plant communities by displacing native flora, changing community structures, and disrupting ecological functions in many Florida ecosystems (Overholt et al. 2014). *Dioscorea bulbifera* infestations have progressively increased from 23 counties (Langeland and Craddock 1998) to 29 counties (Wheeler et al. 2007), and more recently to 65 of the 67 counties of Florida (Croxton et al. 2011). *Dioscorea bulbifera* vines not only grow very rapidly but also branch profusely (M. Rayamajhi, unpublished data) and in this process, vines can form solid canopies that limit light penetration, exert physical weight, collapse supporting vegetation, and ultimately result in the mortality of the plants underneath (Center et al. 2013; Schmitz et al. 1997). Depending on the stage of invasion, a *D. bulbifera* infestation may range from a single vine to a continuous patch of numerous vines covering several hectares.

The typical phenology of *D. bulbifera* consists of an annually repeated cycle of growth and dormancy (Coursey 1967). Its herbaceous vines that climb from the soil surface by twining counterclockwise on supporting structures such as shrubs and trees can grow up to 30 m (98 ft) (Ramser et al. 1996) and reach the upper tree and shrub canopies within each growing season. Growth from subterranean tubers or bulbils that have dropped to the ground begins in early spring and ends in late fall in Florida (Center et al. 2013; Overholt et al. 2003; Schultz 1993). During the active growing phase, the majority of the plant consists of aboveground stems and leaves; the dormant phase is represented by the perennial tubers (Coursey 1967). Stem growth at the beginning of the active phase can be very rapid, up to 15 cm d^{-1} (6 in d^{-1}) (Coursey 1967). Hammer (1998) claimed the observance of *D. bulbifera* seed capsules in Florida while others have noted that it rarely flowers in Florida and when it does, produces only female flowers (Overholt et al. 2014). Therefore, its mode of propagation in Florida is solely vegetative from bulbils. These bulbils, also referred to as "air potatoes" or "air yams," are produced in the axils of alternately arranged leaves (Ramser et al. 1996; Wunderlin and Hansen 2003). There is high intraspecific polymorphism in *D. bulbifera*, especially in the bulbil morphology (Ramser et al. 1996). Based on Martin (1974), *D. bulbifera* produces two distinct bulbil types (described as races): an African type characterized by a light to dark brown color with rough skin, and an Asian type that is tan colored with smooth skin; both types of bulbils are found in discrete or mixed populations in Florida (Overholt et al. 2014). More recently, Croxton et al. (2011) determined that both bulbil types in Florida originated from Asia. These morphotypes can occur as discrete or mixed populations in a given site and both possess similar vine, leaf, and growth attributes in Florida (M. Rayamajhi, unpublished data). The number of bulbils produced per plant varies and the fresh biomass of individual bulbils ranges from < 1 g (0.04 oz) to 1,042 g (M. Rayamajhi, unpublished data). Bulbils disseminate to new areas mainly through anthropogenic means (Schultz 1993), hurricane-strength wind (Horvitz et al. 1998), and water currents along streams.

Land managers deploy cultural, mechanical, and herbicidal control methods for *D. bulbifera* management in Florida (Overholt et al. 2014). These methods alone are inadequate, inefficient, and not cost-effective for long-term suppression of this weedy vine (Wheeler et al. 2007). Cultural methods involving subterranean tuber removal and annual bulbil roundups by land managers and volunteer groups are frequently employed to bring public attention to the problem while removing potential propagules from the site. These events generally take place during winter when the vines have senesced and most bulbils have fallen onto the ground. This cultural method aims to minimize vine recruitment in existing infestations while reducing the spread of vegetative propagules to new landscapes. During these roundup events, although many bulbils that are readily visible are collected and removed from the site, smaller and less-visible bulbils often remain undetected because they are still attached to the vines or are hidden in duff layers on the ground. The potential for recruitment and establishment from these smaller bulbils has not been determined.

The current study was designed to establish baseline data on the effect of bulbil biomass on the growth rate, biomass, and resource partitioning of recruited plant in order to identify any biological attributes that could be exploited in its management efforts. The working objectives of this study were designed to address the following questions:

1. Are the two *D. bulbifera* morphotypes found in Florida similar in terms of growth and biomass?
2. Does the biomass of the parental bulbils (bulbils used in the experiments) affect
   a. the longevity, vine length, seasonal growth rates, biomass, and quantity of subterranean tubers, leaves, and bulbils produced by recruited plants?
   b. the allocation of total biomass to the four (tuber, stem, leaf, and bulbil) major components?
3. Are there identifiable invasive biological attributes in the life stages that can be exploited in its management scheme in Florida?

Materials and Methods

Research Site. The study reported herein was conducted in an open field at the Invasive Plant Research Laboratory (U.S. Department of Agriculture–Agricultural Research Service) at Fort Lauderdale, FL. The prevailing soil type was Margate fine sand, siliceous hyperthermic Mollic Psammaquent, with less than a 1% slope as reported in Tipping et al. (2008). The experiment first conducted in 2012 was repeated during 2013 as described below.

***Dioscorea bulbifera* Propagules.** Vegetative propagules of two morphologically different bulbil types, hereafter referred to as "brown" (possessing brown skin and rough surface with numerous tubercles) and "tan" (tan skin with relatively smooth surface and fewer tubercles) morphotypes were used for both experiments. Bulbils were collected from various locations in southern Florida and sorted into four fresh bulbil biomass groups, hereafter referred to as "parental bulbil biomass categories I–IV"(abbreviated as PBBCs I–V = four bulbil biomass treatments). Maintaining exact biomass of individual bulbils in corresponding PBBCs between 2012 and 2013 was not possible due to inherent differences in biomass and sizes of the field-collected bulbils. The mean masses of PBBCs used in the experiments were as follows: tan morphotype, I = 3.94 ± 1.34 g, II = 25.04 ± 5.43 g, III = 90.01 ± 16.72 g, IV = 212.22 ± 32.12 g; and brown morphotype, I = 3.46 ± 1.14 g, II = 25.00 ± 5.87 g, III = 119.80 ± 14.02 g, IV = 265.30 ± 22.89 g. Each of the four PBBCs within a morphotype was represented by six bulbils for each of the 2012 and 2013 experiments, i.e., 2 morphotypes × 4 PBBCs × 6 bulbils = 48 bulbils yr^{-1}.

Experimental Plots. Two 24 by 20–m plots, one for each of the two bulbil morphotypes, were delineated and the ground was covered with black tarp to keep other weeds from emerging and competing with the *D. bulbifera* vines in the experiments. Twenty-four metal poles that extended to a height of 2 m were installed at 1-m intervals along the 24-m side of each plot. In each plot, two posts located at the opposite ends at a 20-m distance from each other were connected with a plastic-coated cable to create a trellis. Similar trellises were created for each of the 24 paired poles per plot. A 20 by 20 by 20–cm hole was dug at the base of each of the opposite posts on both sides of plots, resulting in 24 holes in each of the two plots. Twenty-four bulbils of each of the two morphotypes, comprising four treatments each with six replicates were randomly assigned and planted individually into one of the 24 holes. Bulbils were planted during the last week of February. Each hole was filled with predominantly organic forest soils collected from Miami Dade County, Florida. Vines originating from planted bulbils were allowed to grow vertically by twining around the pole and then guided horizontally along the trellis following the natural twining behavior of the plant. Vines reaching the end of the 20-m trellis were guided toward a backward direction on the same trellis to allow continued growth during the season. The whole experiment was repeated in 2013. The same plots, posts, cables and holes were used for the 2013 year, using the same planting procedure and timing. However, the soils from the planting holes were replaced with freshly collected forest soils from the same location as for year 2012.

Data Accession. Bulbil planting, initial sprouting, complete senescence, and whole-plant harvesting dates were recorded by plant in both years. Senesced leaves and detached bulbils were gathered every 2 wk and stored in paper bags labeled by plant and added to the corresponding final biomass obtained at the final harvest after complete senescence of the plant; a few green vines that did not senesce were harvested during the last week of December in both months. Subterranean tubers were harvested, counted after washing off soil particles in running water, and recorded by plant. Other parameters recorded by plant included the (1) number of stem(s) arising from ground, (2) number of branches, (3) length of the leader vine that arose from the bulbil, (4) length of branches that arose from the leader vine, and (5) total numbers of leaves and bulbils. All plant materials were oven-dried at 70 C to a constant dry weight and then the final dry weight was recorded by plant.

Data Analyses. The following dependent variables were calculated for use in data analyses:

1. Vine longevity period: Number of days between propagule sprouting and complete leaf and vine browning date within an air potato growing season.
2. Vine longevity-based growth rate (VLGR): Total stem length (leader + branches measured on the final harvest day)/longevity measured in days.
3. Leaf and bulbil densities (number of leaves or bulbils per unit of linear length of vine): Total vine (main vines + branches) length of a plant produced by a parental bulbil/number of leaves or bulbils borne by that plant.

Parental bulbils used in the experiments were collected from a population of field-grown plants in Florida. However, individual bulbils included in bulbil biomass categories were randomly chosen from a pool of similarly sized bulbils. Shapiro-Wilk's normality tests were performed on all independent and dependent variables by morphotypes for both 2012 and 2013 experiments. Overall normality tests on the pooled populations of bulbils constituting four PBBCs, as well as dependent variables, failed as expected. Therefore, the data on independent (PBBCs I–IV) and dependent (growth, biomass, and quantity of tubers, stems, branches, leaves, and bulbils generated by bulbils in PBBCs I–IV) variables were natural log–transformed (Ln-transformed) to stabilize the variances prior to performing further analyses (correlations, regressions, and mean separations). Spearman's correlation tests between the independent and dependent variables were performed using natural log–transformed data within morphotypes from both 2012 and 2013 experimental years.

The effects of experiment years were not included in the model. Morphotypes and PBBC were two independent variables and their main effects and interactions were tested on pooled corresponding dependent variables from 2012 and 2013 experiments by using the GLM procedure (SAS 2011). In this case, the morphotype effects were considered fixed while PBBC effects were considered random. Main effects or interaction terms deemed insignificant ($P > 0.05$) in the model were dropped and only significant ($P \leq 0.05$) terms were included in further analyses of variance. Multiple analysis of variance was applied to assess PBBC (I–IV) effects on dependent variables. The proportion of biomass allocated by the plants to four major components of *D. bulbifera* plants (tuber, stem, leaf, and bulbil) presented herein were arcsine transformed for analyses of variance and mean separations but the data presented on figures and tables are based on the nontransformed percentages. Main effects of independent variable were analyzed using Waller Duncan's multiple range test procedure in SAS (SAS Institute 2011).

In order to identify one or more attributes in the life stages of *D. bulbifera* assumed to contribute to its invasiveness in Florida, we examined correlations among dependent variables, especially of total stem length, with other directly related variables (growth rates, biomass, and quantities of tubers, stems, branches, leaves, and daughter bulbils) by performing Spearman's correlation coefficient test. This provided insight into the major invasive attributes of *D. bulbifera* occurring in Florida.

Results and Discussion

Correlations. The coefficients of correlation between the parental bulbil biomass and each of the dependent variables: total stem length, VLGR, total dry biomass, quantities of tubers, main stems arising from each bulbil, and leaves and bulbils generated by plants in each of the two morphotypes showed similar trends for both 2012 and 2013 (Table 1). These similarity trends between 2 yr justified combining corresponding data from both years by morphotype for further analyses needed to determine treatment effects on the dependent variables of interest. The positive correlation between the bulbils in PBBCs I–IV and total dry biomass, total stem length, VLGR, and the quantity of leaves and daughter bulbils was relatively strong for both morphotypes (Table 1). However, the correlation between the bulbils in PBBC and the quantities of subterranean tuber and the main stems per plant was very weak (Table 1). This indicated that the biomass of parental bulbil did not affect the number of underground tubers produced by plants during the growing season.

Effects of Parent Bulbil Biomass. Vine longevity and number of tubers per plant was affected neither by morphotypes nor the bulbil biomass in PBBCs (Table 2). The main effects of morphotypes and the interaction term (Ln-morphotypes by Ln-PBBC) were also not significant (at $P \leq 0.05$) for all tested dependent variables. These findings show that, despite differences in the bulbil morphology, plants generated by both brown and tan

Table 1. Correlation coefficient[a] (r) trends between fresh weight of the parent bulbils of *D. bulbifera* included in four parental bulbil biomass categories and the resulting dependent variables in 2012 and 2013 experimental years.

	2012		2013	
Dependent variables	r (P) values	df	r (P) values	df
Brown morphotype[b]				
Total stem length (cm plant^{-1})	0.903(0.0000002)	24	0.912(0.0000002)	24
VLGR[c] (cm d^{-1})	0.905(0.0000002)	24	0.904(0.0000002)	24
Total dry biomass (g plant^{-1})	0.904(0.0000002)	24	0.927(0.0000002)	24
Number of tubers plant^{-1}	−0.018(0.9300000)	24	0.149(0.4840000)	24
Number of main stems plant^{-1}	0.133(0.5310000)	24	0.275(0.1890000)	24
Number of leaves plant^{-1}	0.761(0.0000002)	24	0.814(0.0000002)	24
Number of daughter bulbils plant^{-1}	0.901(0.0000002)	24	0.812(0.0000002)	24
Tan morphotype[d]				
Total stem length (cm)	0.742(0.0000104)	21	0.821(0.0000002)	24
VLGR (cm d^{-1})	0.726(0.0000867)	21	0.807(0.0000002)	24
Total dry biomass (g plant^{-1})	0.819(0.0000002)	21	0.890(0.0000002)	24
Number of tubers plant^{-1}	0.247(0.2760000)	21	0.138(0.5150000)	24
Number of main stems plant^{-1}	0.078(0.7330000)	21	−0.037(0.8600000)	24
Number of leaves plant^{-1}	0.574(0.0066100)	21	0.382(0.06490	24
Number of bulbils plant^{-1}	0.694(0.0004000)	21	0.639(0.000773)	24

[a] Coefficient values on the rows and columns closer to 1.0 show strong positive correlation between the fresh weight of the propagated bulbils with the dependent variable and vice versa.

[b] Brown morphotype = plants producing brown skinned bulbils and rough surfaces marked by many tubercles.

[c] Abbreviation: VLGR, vine longevity-based growth rates.

[d] Tan morphotype = plants producing tan skinned bulbils with relatively smooth skin.

morphotypes exhibit similar trends in terms of growth and biomass production. However, the main effect of PBBC was significant ($P \leq 0.05$) on the dependent variables included in the test (Table 2). Hence, the main effects of morphotypes and the interaction terms were dropped from the model and only main effect of PBBC was used in further analysis. This allowed us to combine data from corresponding variables in brown and tan morphotypes while comparing differences among dependent variables in four bulbil biomass categories.

Vine Attributes, In general, *D. bulbifera* vines begin to senesce and die every year during November and December in northern and southern Florida, respectively (M. Rayamajhi, unpublished data). The plant appears to have two phases in its annual growth cycle. During the initial phase, sprouts emerge from the bulbils while a tuft of fleshy roots extends into the soil. Plants at this first stage appear to allocate resources toward linear growth and branching of the vine stems so as to develop and support a large number of leaves within a very short period of time. A similar growth pattern has been reported for exotic vine *Dioscorea oppositifolia* L. in North America, whose growth rate decreased as the growing season progressed (Beyerl 2001; Mueller et al. 2003). The initial fast growth presumably ensures an increase in plant's photosynthetic ability and exacerbates its smothering effects on the supporting vegetation. During the second phase, linear growth appears to slow and the vines begin to allocate resources toward developing bulbils at the leaf axils. The first phase represents an active growth period whereas the second phase represents a period of bulbil production that ensures the availability of vegetative propagules for dispersal during the ensuing dormant period.

The differences in the mean longevity of vines generated by PBBCs I–IV within growing seasons was not significantly different ($P > 0.05$) and had a narrow longevity range of 181 to 198 d (Table 3). However, the VLGRs of vines generated by the bulbils in PBBC were significantly ($P \leq 0.05$) different. The mean VLGR of vines generated from PBBCs I–IV ranged from 1.56 to 11.78 cm d^{-1} (maximum 25.19 cm d^{-1}) (Table 3). As noted here, the VLGRs of *D. bulbifera* vines increased with the biomass of the parental bulbils. Without an indication of the propagule source (subterranean tubers or bulbils) that produced vines, growth rates of the *D. bulbifera* plant has been reported to be as much as 15 cm d^{-1} (Coursey 1967) compared to a maximum mean of 25 cm d^{-1} for largest

Table 2. P values showing the effects of two bulbil morphotypes[a] and four parental bulbil biomass categories[b] on the dependent variables of *D. bulbifera* plants during two growing seasons in the 2012 and 2013 experimental years.

	Independent variables		
Dependent variables	A[a] (df = 1)	B[b] (df = 3)	A × B (df = 3)
Vine longevity (d)[c]	0.9396[e]	0.4717	0.9212
Total vine length (cm $plant^{-1}$)[c]	0.1631	< 0.0001	0.7558
Vine longevity-based growth rates (cm d^{-1})[c]	0.1365	< 0.0001	0.7256
Dry biomass (g $plant^{-1}$)[c]			
Total	0.0657	< 0.0001	0.6683
Tubers	0.0334	0.0008	0.2847
Stems	0.1217	< 0.0001	0.6963
Leaves	0.0778	< 0.0001	0.6138
Daughter bulbils	0.3741	< 0.0001	0.7179
Biomass allocation (% of total)[d]			
Tubers	0.1896	< 0.0001	0.3386
Stems	0.4775	0.0035	0.5390
Leaves	0.1607	< 0.001	0.1423
Daughter bulbils	0.8133	< 0.0001	0.4594
Number $plant^{-1}$[c]			
Tubers	0.2195	0.1727	0.1557
Main vines			
Leaves (or vine nodes)	0.7863	< 0.0001	0.2212
Daughter bulbils	0.1043	< 0.0001	0.4681
Densities (cm^{-1} of vine length)[c]			
Number of leaves	0.0914	< 0.0001	0.6713
Number of bulbils	0.0017	0.0006	0.3689

[a] A = Morphotypes (brown and tan).

[b] B = Parental bulbil biomass categories I–IV from 2012 and 2013 experiments.

[c] Count, weight, and rate values were natural log–transformed prior to the analysis presented herein.

[d] Proportional biomass data were arcsine-transformed prior to the analyses presented herein.

[e] P values ≤ 0.05 indicate significant effects of parental bulbils in parental bulbil biomass categories on the dependent variables.

Table 3. Seasonal growth attributes of the two morphotypes of *D. bulbifera* plants generated by the four parental bulbil biomass categories collected from southern Florida during 2012 and 2013 experimental years.

	PBBC[a,b]				
Dependent variables	I	II	III	IV	Data range
Vine longevity period (d)	185.88 a[c]	188.90 a	191.13 a	198.30 a	93.00–227.00
Tot stem length (cm $plant^{-1}$)	290.20 d	829.90 c	1,658.50 a	2335.80 a	23.00–5,088.70
VLGR[a] (cm d^{-1})	1.56 d	4.40 c	8.68 b	11.78 a	0.24–25.19
Densities cm^{-1} of stem					
Leaf	0.63 a	0.19 b	0.11 c	0.10 c	—
Daughter bulbil	0.06 a	0.06 a	0.06 a	0.05 a	—

[a] Abbreviations: PBBC, parental bulbil biomass category; VLGR, vine longevity-based growth rate.

[b] Based on the combined corresponding values of both morphotypes and experimental years 2012 and 2013 (n = 10 to 12/PBBC).

[c] Numbers on the rows and columns represent treatment means. Means within a row followed by different letter(s) are significantly different from each other at $P \leq 0.05$ as per Waller Duncan's multiple range test.

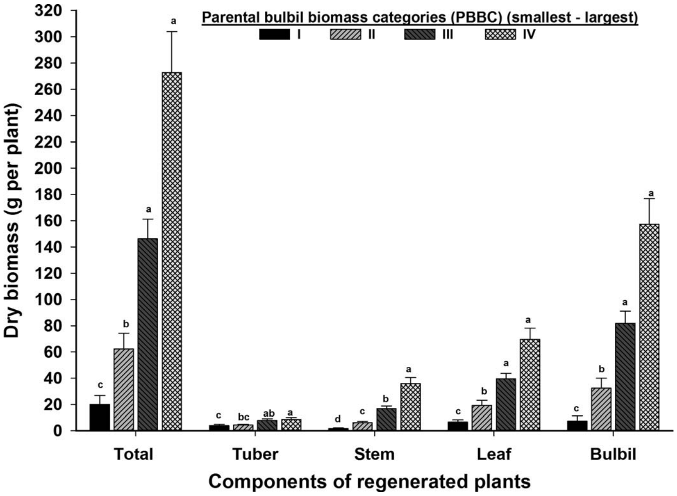

Figure 1. Total dry biomass (g plant^{-1}; mean ± SE) and its distribution (g plant^{-1}; mean ± SE) in four major components (tuber, stem, leaf, and bulbil) of plants generated by the parental bulbil biomass categories (PBBCs) I–IV of *D. bulbifera*, combined for both morphotypes (brown and tan) and experimental years (2012 and 2013). Each vertical bar represents the mean and standard error of the mean ($n = 21$ to 24) of the respective plant component generated by parental bulbils in PBBCs. Means followed by different letter(s) among parental bulbils in four PBBCs within a given plant component are significantly different from each other at $P \leq 0.05$ as per Waller Duncan's multiple range test.

parental bulbils in our experiment. This type of aggressive seasonal growth exhibited by *D. bulbifera* has been described by Nehrling (1933, 1944) as second only to kudzu, *Pueraria montana* var. *lobata* (Willd.) Maesen & S.M. Almeida (Nehrling 1933, 1944), an invasive vine of Japanese origin affecting vast natural areas in certain parts of North America (Forseth and Innis 2004).

Seasonal (Annual) Biomass. Total dry biomass (rooted tubers, stem, leaves, and bulbils) increased with the biomass of the parental bulbils in both morphotypes (Figure 1). The mean of the total biomass of plants generated by the bulbils in PBBCs I–IV of the two *D. bulbifera* morphotypes ranged from 20.1 to 272.7 g plant^{-1} (actual range, 0.52 to 555.8 g plant^{-1}). In both *D. bulbifera* morphotypes, actual dry biomass allocation into subterranean tubers, stems, leaves, and bulbils increased with the increase in the biomass of the parental bulbils (Figure 1). Overall, *D. bulbifera* dry biomass per plant appeared small considering the vines' total fresh weight, their ability to scale long distances, cover large surface areas, and cause smothering effects on supporting vegetation. The moisture content in the subterranean tubers, stems, leaves, and bulbils was 74, 77, 81, and 77%, respectively, and these high proportions of moisture contents in the fresh biomass of plant components resulted in small amount of total dry biomass of the plant (M. Rayamajhi, unpublished data).

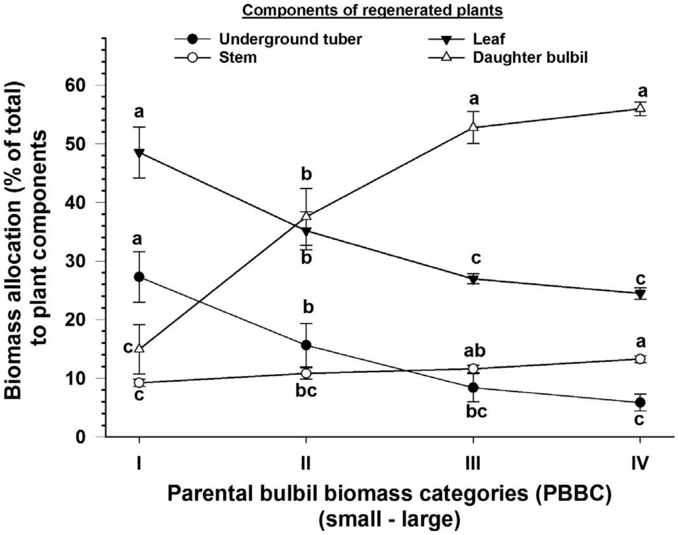

Figure 2. Proportional (%) allocation (mean ± SE) of total biomass to four major components of plants generated by each of the four parental bulbil biomass categories (PBBCs) of *D. bulbifera* combined for both morphotypes (brown and tan) and experimental years (2012 and 2013). Means ($n = 21$ to 24) of plant components across PBBCs I–IV represented by different letter(s) are significantly different from each other at $P \leq 0.05$ as per Waller Duncan's multiple range test.

Even though the distribution of total seasonal biomass among tubers, stems, leaves, and bulbils increased with the biomass of the parental bulbils, the proportions (%) of the total biomass allocated to these four plant components was different (Figures 1 and 2). Vines generated by smaller parental bulbils (PBBCs I and II) allocated large proportions of total biomass to leaves (e.g., 35 and 48%) and subterranean tubers (16 and 27%) compared to stems (9 and 11%) and bulbils (15 and 38%) (Figure 2). In contrast, vines generated by large parental bulbils (PBBCs III and IV) allocated greater proportions of their total biomass to bulbils (53 and 56%) and leaves (27 and 25%) compared to stems (12 and 13%) and subterranean tubers (8 and 6%) (Figure 2). *Dioscorea bulbifera* vines produced from smaller parental bulbils allocated greater biomass to subterranean tubers, which may ensure perennial establishment at the site, while those vines generated by larger parental bulbils invested a greater proportion of resources to generate relatively large biomass and quantities of leaves and bulbils that can blanket supporting structures in addition to enhancing the ability to recruit new plants.

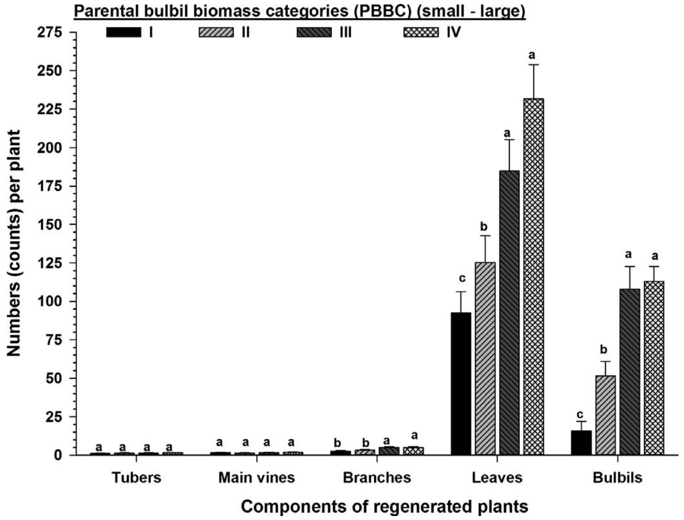

Figure 3. Mean (± SE) number of the four components (tuber, stem, leaf and bulbil) per plant, generated by four parental bulbil biomass categories (PBBCs) of *D. bulbifera* combined for both morphotypes (brown and tan) and experimental years (2012 and 2013). Mean ($n = 21$ to 24) units of a given plant component representing a PBBC followed by different letter(s) are significantly different from each other at $P \leq 0.05$ as per Waller Duncan's multiple range test.

Quantity of Plant Components. Data on the quantities of *D. bulbifera* plant components are presented in Figure 3. Each plant component plays an important role in one or more aspects of its ability to exploit available resources within an invaded plant community. While the tubers contribute to the perennial habit, the stem growth contributes to the linear length of the vines that bear branches with relatively thin leaves and bulbils, which in turn contributes to plant's photosynthetic and seedling recruiting efficiencies. The number of subterranean tubers and main vines was not influenced ($P > 0.05$) by the biomass of the parental bulbil. The mean number of tubers and main vines produced by smallest to largest bulbils in PBBC ranged from 1.1 ± 0.18 to 1.5 ± 0.12 and 1.7 ± 0.19 to 1.9 ± 0.21, respectively. However, the number of branches, leaves, and daughter bulbils increased significantly ($P \leq 0.05$) with the biomass of the parental bulbil. The mean number of branches, leaves, and bulbils borne by the main vines arising from smallest to largest PBBC ranged from 2.5 ± 0.44 to 5.0 +0.62, 92.7 ± 0.13.6 to 231.7 ± 22.3, and 15.8 ± 6.17 to 113.0 ± 9.8, respectively. The leaf densities (number of leaves cm^{-1} linear length of vine) on vines generated by the PBBCs I–IV showed an inverse relationship whereas the linear density of bulbils (number of bulbils cm^{-1} linear length of vine) remained uninfluenced by the bulbil biomass in PBBCs (Table 3). Approximately 94% of *D. bulbifera* bore bulbils (data not shown) with a linear density of 0.05 to 0.06 bulbils cm^{-1} of stem (Table 3). Thomas et al. (2006) studied the invasion potential of a congener invasive yam *D. oppositifolia* in Illinois and documented that only 36% (18 out of 50 plants) of the plants studied produced bulbils and the linear density was ca 0.15 bulbils cm^{-1}.

The above data, particularly the relationship between the number of leaves and bulbils per plant in our study are interesting since they showed very strong positive correlation. *Dioscorea bulbifera* vines generated from larger parental bulbils in PBBC IV bore approximately one bulbil at the axil of every second leaf (232 leaf axils and 113 daughter bulbils) whereas vines generated by the smallest parental bulbils (PBBC I) bore one daughter bulbil at the axil of every sixth leaf (93 leaf-axils and 16 daughter bulbils). The leaf density on vines decreased with the increase in vine length and vice versa, whereas the densities of daughter bulbils was not influenced by the parental bulbils used in PBBCs that generated those vines.

Invasive Attributes and Management. A total of 154 species of invasive exotic vines have been listed for North America (www.invasive.org/species/vines.cfm). Vines represent about 9% of the invasive plants in the eastern United States and *D. bulbifera* is one of the herbaceous vines in that list that perpetuates in the form of perennial subterranean tubers (Bargeron et al. 2003). Despite its status as a Category 1 noxious weed in Florida, *D. bulbifera*'s invasive attributes in its life stages have not been documented. Herein, we discuss *D. bulbifera*'s invasive biological attributes that can be exploited to reduce its invasiveness in Florida.

The current study showed that bulbils with a biomass of less than 1 g are capable of recruiting new plants and initiating new infestations. In this study, we also established that the growth rate, vine length, total biomass, and number of leaves and daughter bulbils per plant increases with the biomass of the parental bulbils generating those plants. The ability (1) to grow at a faster rate and produce longer vines that can effectively blanket and smother supporting vegetation and (2) produce a large number of bulbils within a growing season may be considered invasive attributes in this species.

Correlation coefficient of dependent variables showed stronger positive correlation of the total vine length with other dependent variables, namely, growth rates, total biomass, degree of branching, and number of leaves and daughter bulbils (Table 4). Of these, vine length, degree of branching, and quantities of leaves are directly related to the smothering effect on the structures it has blanketed, whereas the biomass and quantity of bulbils are related to

Table 4. Correlation coefficients (*r* values) showing overall relationship of total vine length with each of the listed dependent variables generated from the parent bulbils in PBBCs[a,b] of both morphotypes[c] of *D. bulbifera* plants in both 2012 and 2013 experiment years.

Dependent variables	*r* values[d]	P values	*N*
Total dry biomass (g plant^{-1})	0.960	0.0000002	93
VLGR (cm d^{-1})	0.983	0.0000002	93
Number of branches plant^{-1}	0.518	0.0000002	93
Number of leaves plant^{-1}	0.858	0.0000002	93
Number of daughter bulbils plant^{-1}	0.880	0.0000002	93

[a] Abbreviations: PBBC, parental bulbil biomass categories; VLGR, plant longevity-based growth rate.

[b] PBBCs from both morphotypes and experiment years (2012 and 2013) were pooled for this analysis.

[c] Brown morphotypes: plants producing brown skinned bulbils with rough surfaces marked by series of tubercles; tan morphotypes: plants producing tan skinned bulbils with relatively smooth surfaces and fewer tubercles.

[d] *r* values on the rows and columns closer to 1.0 indicate strong positive correlation of total vine length with the tested dependent variables.

the recruitment of seedlings and possibly initiation of new infestations.

Because the bulbils are produced at the leaf axils, reduction in the vine length should also reduce the quantity and biomass of both leaves and bulbils. Natural enemies that feed or damage the leaves and growing tips may be able to limit vine length and hence reduce the invasive potential of *D. bulbifera* in Florida. This assumption is supported by Atkinson et al. (2014), who reported that reduced photosynthetic surfaces from chronic defoliation of plants negatively affects carbohydrate reserves and reduces growth rates of affected plants.

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