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Measuring summer patterns of ascospore release by saltmarsh fungi

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One potentially important type of flux from standing-decaying marshgrass is the production and release of ascospores. The most extensive measurements of ascospore release from the principal marshgrass (*Spartina alterniflora*, smooth cordgrass) of saltmarshes of the eastern coastal United States involved an arbitrary, weeklong period of wet incubation of leaf-blade samples. We examined the possibility that shorter incubations would yield higher estimates of hourly rates of ascospore release, testing wet incubations of 3 to 71 h, using standing-decaying leaf blades of smooth cordgrass from low on living shoots and high on dead shoots. Incubations of 31 h appeared to be optimal. Species compositions of ascospores expelled from the two leaf types were distinctly different: high leaves yielded primarily a *Mycosphaerella* species or *Phaeosphaeria halima*; low leaves yielded primarily *Phaeosphaeria spartinicola* or the *Mycosphaerella* species. All of these species consistently exhibited high coefficients of variation (>100%) for their mean rates of release of ascospores. Only the *Mycosphaerella* species on high leaves gave evidence of a delayed onset of ascospore expulsion during incubation, and this evidence was equivocal. Grand mean rates of ascospore release for *P. spartinicola* and the *Mycosphaerella* species were, respectively, 106 and 238 spores cm^{-2} abaxial leaf area h^{-1}.

Key Words——ascomycetes; ascospore-expulsion rate; marshgrass; *Mycosphaerella*; *Phaeosphaeria*.

Flow to secondary production by ascomycetous fungi is the primary destiny of dead shoots of smooth cordgrass (*Spartina alterniflora* Loisel), the highly photosynthetically productive grass of eastern USA saltmarshes (Newell, 1996; Newell and Porter, 2000), prior to movement into the marsh's trophic relay (Kneib, 1997). Newell and Wasowski (1995) attempted to measure one form of ascomycetous production from smooth cordgrass, as rate of output of meiospores (ascospores). They recorded the rate of deposition of ascospores onto target coverslips for wetted, naturally-decaying leaf blades. They used one arbitrarily chosen standard incubation period (168 h) for the ascospore-releasing blades. Newell and Wasowski (1995) counted ascospores only for the two species of ascomycetes (*Phaeosphaeria spartinicola* Leuchtmann and *Buergenerula spartinae* Kohlm. & Gessner) that they detected by direct-microscopic enumeration as the major producers of mature ascomata in naturally decaying blades low on partially living shoots. It was subsequently discovered that a prominent ascospore-producing species in standing-decaying smooth-cordgrass blades is *Mycosphaerella* sp. 2 (of Kohlmeyer and Kohlmeyer, 1979), which has smaller, more cryptic ascomata than the ascomata of *P. spartinicola* with which they are often mixed (Newell and Porter, 2000). We report here our attempt to improve interpretability of the ascospore-capture technique as used with saltmarsh grasses; the resultant data add to the currently meager definition of the spatiotemporal pattern of ascospore expulsion from naturally-decaying smooth-cordgrass blades (Newell and Wasowski, 1995; Newell and Wall, 1998; Newell et al., 2000a, b). We measured rates of expulsion (spores cm^{-2} leaf abaxial surface h^{-1}) for three species of ascomycetes, including *Mycosphaerella* sp. 2. We used five periods of leaf incubation between initial wetting and 71 h, to determine whether or not rates were stable over this range of durations of leaf-blade wetness, and we sampled four different smooth-cordgrass swards and standing-decaying leaves of two distinct types.

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Materials and Methods

Sites All leaf blades were collected within smooth-cordgrass (*Spartina alterniflora*) marshes of Sapelo Island (31°23'N, 81°17'W) (Chalmers, 1997; Pomeroy and Wiegert, 1981). Site A was along the creek bank of Southend Creek (Doboy Sound watershed: Chalmers, 1997) (mature shoots approximately 1.75 m tall). Site B was about 20 m away from site A, in intermediate-height marsh (mature shoots about 1 m tall). Site C was at Cabretta Island in intermediate-height marsh (Atlantic Ocean watershed). Site D was in intermediate-height marsh alongside Nannygoat Beach road, near Dean Creek (Doboy Sound watershed). All four sites had concentrations of detritivorous periwinkles (*Littoraria irrorata*) ≤ average for Sapelo marshes ($\bar{x} = 24 \pm 25$ m^{-2}; Newell and Wall, 1998).

Sampling Twenty standing-decaying leaf blades of

smooth cordgrass were collected at each site during Jun – Aug, 1999 by severing them from their sheaths at the ligule (one blade collected per shoot). The amount of time since the last rain was recorded for each collection. Leaves of two types were collected: (i) dead blades on wholly dead shoots (dead-on-dead, DOD), from near the tops (about 3/4 of total height) of the shoots; (ii) dead blades (the first or second below the current yellow-green, senescent blade) on partially living shoots (dead-on-live, DOL), from near the bases of the shoots (leaves die in sequence from low to high on shoots: Newell et al., 1998). DOD blades were collected at the four sites first (10 Jun – 30 Jun), because wholly-dead shoots lose their blades to fungal decay and the shoots fall to the sediment in summer (Newell et al., 1996, 1998). Subsequently the DOL blades were collected (7 Jul – 2 Aug).

Blades collected were selected for absence of large patches of blackened areas (*Buergenerula spartinae*; Newell and Porter, 2000) and for uniformity of coverage by "black-peppered" appearance [*P. spartinicola* and *Mycosphaerella* sp. 2 (of Kohlmeyer and Kohlmeyer, 1979)] (Newell and Porter, 2000). We selected against the presence of *B. spartinae* because it tends to ooze its ascospores out of the blades, rather than expelling them forcefully away (Newell pers. obs.). As a consequence of this selection against *B. spartinae*, our findings for rate of ascospore output do not represent total ascospore output. Blades were immediately returned to the laboratory and stored air-dry until processed (within 48 h).

Ascospore expulsion Rates of ejection of ascospores by the predominant ascospore-expelling ascomycetes in our sampled smooth-cordgrass blades were measured by the ascospore-capture technique of Newell and Wall (1998; after Aylor and Anagnostakis, 1991; Newell and Wasowski, 1995). Briefly, this involved incubation at 20 °C of wetted and drained 8-cm lengths of blade (taken from between 3 and 11 cm distal to the ligule) in damp chambers with target coverslips placed 7 mm beneath the abaxial surface (location of the ascomycete ostioles) of the incubating blade. The width of each blade piece was measured at its center. The incubation temperature was chosen: (i) for optimization of comparability to a 3-y, 4-season data set for ascospore release from standing-decaying smooth cordgrass in which all incubations were for 72 h at 20 °C (Newell, unpublished); and (ii) because 20 °C is a common midrange air temperature for Sapelo marshes in early summer (Chalmers, 1997). The two ends of the 8-cm pieces were in contact with deionized-water during incubation, so that the pieces stayed saturated with water throughout the incubation periods.

Modifications of the Newell and Wall (1998) procedure were: (i) incubations were under 12/12-h on/off, $251 \pm 32\ \mu E\ m^{-2}\ s^{-1}$ photosynthetically available radiation (PAR; fluorescent bulbs; Li-Cor LI-188B integrating photometer) (except DOD blades for site A: $30\ \mu E\ m^{-2}\ s^{-1}$); and (ii) a series of incubation times were used (3, 23, 31, 46, and 71 h). Four replicate leaf pieces (1 per incubation chamber) were used for each incubation time. Spores on each target coverslip were counted at × 125 in non-selectively chosen fields along the line representing the center of the longitudinal axis of the leaf piece (Wild M8 stereomicroscope, with an eyepiece grid, field size 1 mm^2, five fields counted per coverslip) for the two most prevalent species from each type of leaf: DOD, *Mycosphaerella* sp. 2 (of Kohlmeyer and Kohlmeyer, 1979) and *Phaeosphaeria halima* (Johnson) Shoemaker & Babcock; DOL, *P. spartinicola* and *Mycosphaerella* sp. 2. (Piquant aside: Species of *Phaeosphaeria* and *Mycosphaerella* are common as pathogens of commercial grasses: Cunfer and Ueng, 1999). For counting of *Mycosphaerella* spores at the Wild M8, dark-field observation was used, because these small (ca. $18 \times 7\ \mu m$) hyaline ascospores were often difficult to resolve in bright field, which was used for the other two (brown-spored) species. We tested cotton-blue staining of *Mycosphaerella* spores (Jailloux et al., 1999); the ascospores were too lightly stained to provide improved detectability. Identities of all types of ascospores were confirmed for each coverslip by examination at × 400 (Zeiss interference contrast). Concentrations of spores under the leaf-piece centerline were taken to be representative of concentrations per leaf abaxial area (Newell and Wasowski, 1995), an assumption that appeared valid, since leaf width was not related to spore concentration in most cases (see Results). For rate calculations, we found average spore concentration per leaf-piece area (4 replicate pieces × 5 fields) and divided by incubation time.

Statistical analyses Correlation, regression, and analyses of variance (ANOVA) were performed using SPSS/PC+ Version 5.0 (Norušis, 1992). Significance level was set at $P = 0.05$. Logarithmic transformations were performed to resolve the problem of heteroscedasticity when it was encountered (Sokal and Rohlf, 1995). Mean values herein are shown ± SD (except SE for regression slopes as indicated below).

Results

For rate of ascospore release, there was no significant ($P < 0.05$) interaction found between site and duration of incubation for any of the four species/leaf-types examined. For all of the species/leaf-types except *Phaeosphaeria spartinicola*/dead-on-live (DOL; see Methods), there were significant differences among mean rates of ascospore release among the sites (Table 1), but there were no significant differences among mean rates of ascospore release for the times of incubation (Table 2). All mean rates of ascospore release were associated with large coefficients of variation (CV; $= SD/\bar{x}$), ranging from 0.88 to 3.42 (Table 1). *Phaeoshaeria spartinicola* was observed from dead-on-dead (DOD) samples, but at an overall mean ascospore-release rate that was 18% of that for *P. halima*. Ascospores of *P. halima* were observed from only two of 80 total DOL blade replicates. Other species for which ascospores were rarely observed were: *Hydropisphaera erubescens* (Desm.) Rossman & Samuels (= *Bionectria* sp. of Rossman: Newell and Porter, 2000; see Rossman et al., 1999);

Table 1. Ascospore release[a,b] for four combinations of species and leaf type measured for four sites, and averaged over all incubation times.

Spp./Type[c]	Site A	Site B	Site C	Site D
MY2/DOD	508±1004A	430±1470B	4±10C	12±41C
PH/DOD	6±20C	4±10C	56±65A	15±31B
PS/DOL	103±134A	57±50A	119±181A	141±150A
MY2/DOL	10±16B	25±45B	25±45B	194±319A

[a] $\bar{x}\pm$SD, spores cm^{-2} abaxial leaf surface h^{-1}.
[b] Capital letters designate mean values within rows that are significantly ($P<0.05$, ANOVA+SNK) different from one another ($n=20$ 5-mm^2 fields per mean value).
[c] MY2=*Mycosphaerella* sp. 2; PH=*Phaeosphaeria halima*; PS=*Phaeosphaeria spartinicola*; DOD=dead blades on wholly-dead shoots; DOL=dead blades on partially-living shoots.

Table 2. Ascospore release[a,b] for four combinations of species and leaf type measured at five incubation times, and averaged over all sites sampled.

Spp./Type[c]	Incubation (h)					Grand $\bar{x}$
	3	23	31	46	71	
MY2/DOD	42±149	313±962	605±1711	197±435	36±61	238±904
PH/DOD	23±50	25±56	12±27	24±48	19±31	21±43
PS/DOL	198±216	68±91	98±117	90±116	75±84	106±139
MY2/DOL	169±352	33±54	62±137	27±43	26±46	64±177

[a] $\bar{x}\pm$SD, spores cm^{-2} abaxial leaf surface h^{-1}.
[b] No significant ($P<0.05$) differences among mean values within rows ($n=16$ 5-mm^2 fields per mean value for each incubation time and species/type).
[c] MY2=*Mycosphaerella* sp. 2; PH=*Phaeosphaeria halima*; PS=*Phaeosphaeria spartinicola*; DOD=dead blades on wholly-dead shoots; DOL=dead blades on partially-living shoots.

Buergenerula spartinae; *Pleospora pelagica* Johnson; and two unidentified species. In potentially comparing rates of ascospore output for *P. spartinicola* and *Mycosphaerella* sp. 2, note that the former has an ascospore volume of 4.7×10^3 μm^3, and the latter 1.0×10^3 μm^3, calculated as oblate spheroids.

Regression of concentrations of ascospores on coverslips against hours of incubation were significant for *P. halima*/DOD and *P. spartinicola*/DOL ($P=0.01$ and 0.0004, respectively), but not for *Mycosphaerella* sp. 2 on either leaf type ($P=0.92$ for DOD, 0.14 for DOL). Slopes for the former two species were: *P. halima*, slope=19±8 (SE) spores $cm^{-2}h^{-1}$; *P. spartinicola*, slope=73±20 spores $cm^{-2}h^{-1}$. Slope for *Mycosphaerella* sp. 2, DOL, was 19±13 spores $cm^{-2}h^{-1}$. The highest mean rate of release of ascospores for *Mycosphaerella* sp. 2 for DOD blades was found at 31 h (Table 2), and the mean rate fell sharply to the 71-h point. When regressions of spore accumulation upon incubation time were performed for *Mycosphaerella* sp. 2, DOD, using the period 3–31 h, regression slope was 605±404 spores $cm^{-2}h^{-1}$ ($P=0.14$).

Table 1 shows that *P. halima* had higher rates of ascospore release at sites with lower rates for *Mycosphaerella* sp. 2. However, when data for all DOD samples was included, there was no significant correlation between rates for these two species ($r=-0.11$, $P=0.32$). Neither was there a correlation between rates for the two principal ascomycetes of DOL samples ($r=0.09$, $P=0.39$).

The length of the period without rain preceeding sampling (ranging from 3 h to 7 d) was not significantly correlated to rate of ascospore release for the data as a whole ($r=0.01$, $P=0.81$), nor for either of the two principal ascomycetes of the two types of leaf (*Mycosphaerella* sp. 2/DOD, $r=-0.07$, $P=0.52$; *P. spartinicola*, $r=0.16$, $P=0.16$).

The width of the blade sampled was weakly significantly correlated to rate of ascospore release for the data as a whole ($r=0.12$, $P=0.04$). This was entirely due to correlation of blade width to rates for *Mycosphaerella* sp. 2/dead-on-dead ($r=0.26$, $P=0.02$). There were no other significant correlations of blade width with rates of release for the three other species/blade-types (range, $r=-0.11$ to 0.04, $P=0.33$ to 0.70).

Discussion

One assumption of the method that we used to estimate ascospore-expulsion rates per unit area of abaxial surface of leaf is that the spore concentration per mm^2, along the centerline of the test blades on the coverslip below the

blades, is representative of the rates of output for the whole blade area (Newell and Wasowski, 1995). This assumption would be shown to be false if the width of the blades tested produced an effect upon the concentrations of spores recorded, via wider blades permitting more spore influx to the centerline at angles from near blade edges. We tested this assumption by looking for any correlation between spore concentrations and blade width. For three of four species/leaf-types, there was no significant correlation, suggesting that the methodological assumption is valid. But for *Mycosphaerella* sp. 2/DOD, there was a significant correlation with blade width, explaining 7% (r^2) of the variation in spore-release rates. Since this correlation was found for only one of four cases, it is likely to be due to a weak tendency for *Mycosphaerella* sp. 2 to produce more ascospores in larger, thicker blades, rather than to an invalidity of the methodological assumption.

Newell and Porter (2000) suggested that use of shorter wet-incubation periods than used previously (168 h: Newell and Wasowski, 1995) might lead to higher estimates of ascospore-expulsion rates from standing-decaying smooth cordgrass. This suggestion appears to be correct: average ascospore-release rate for *P. spartinicola* in Sapelo marshes, estimated using 168-h wet incubations of DOL blades in summer at two sites free of shredder snails, was 28 spores $cm^{-2}\,h^{-1}$ (Newell and Wasowski, 1995); our grand mean for *P. spartinicola*/DOL was 106 spores $cm^{-2}\,h^{-1}$ (Table 2). However, the periods 3–71 h gave statistically equivalent rates for *P. spartinicola* in the present work, and by the 31-h point, the mean rate had converged upon the grand mean and the CV appeared to have plateaued at about 100% (Table 2), so 31 h might be a good choice for the wet-incubation period for estimating the hourly rate of ascospore release for *P. spartinicola*.

Thirty-one h appear to be suitable also for *P. halima*/DOD and *Mycosphaerella* sp. 2/DOL (Table 2), but whether this amount of time is appropriate for *Mycosphaerella* sp. 2/DOD remains open to question. Our results hint (but $P=0.14$ for the regression; see Results) that a peak in rates of ascospore expulsion for *Mycosphaerella* sp. 2/DOD may occur at the 31-h point, and that the rates might fall off sharply after 31 h. If this peaking is real (a question that needs more sampling for resolution; see Table 2), then one would conclude that the rate of release of ascospores by *Mycosphaerella* sp. 2 in dead leaves high on dead shoots rises as the period of wetness grows longer, up to 31 h. This would be in contrast to the two *Phaeosphaeria* species, and possibly *Mycosphaerella* sp. 2 on partially living shoots, which showed more stable average rates throughout the 71-h wet incubations (Table 2). Since most wetting events (tides, rain, dew; Newell et al., 1998) would not be expected to last for 31 h, the rates found for *Mycosphaerella* sp. 2/DOD at 31 h may be better considered potential rates than as rates relevant to natural situations.

If the 31-h spore-release peak for *Mycosphaerella* sp. 2/DOD is real, then it would appear that there is a sharp (17-fold) decline by the 71-h point (Table 2). This potential decline is likely to be due to the fact that we used dark field for counting of the ascospores of *Mycosphaerella* sp. 2. The small (about 18×7 μm), hyaline ascospores of *Mycosphaerella* sp. 2 are difficult to identify in bright field at the stereomicroscope. Dark field enhances their detectability, making cytoplasm-filled spores more readily visible. Spores that had germinated and lost cytoplasm to the germ hypha were no longer readily visible in dark field (as determined by comparison to a stereomicroscope with contrast enhancement in bright field). Since all three of the ascomycetes of Table 2 germinate on ascospore-capture coverslips, loss of detectability of *Mycosphaerella* sp. 2 spores in dark field is a likely explanation of the potential decrease in rates of spore release found for *Mycosphaerella* sp. 2. Note that this loss of recognizability could have caused counts of *Mycosphaerella* sp. 2 to be low at points earlier than the 71-h point, at which unreasonably low counts appeared (Table 2).

There was a clear difference in the species composition of ascospores expelled from the two types of standing-decaying blades examined. Those low on living shoots at three of four sites released mostly spores of *P. spartinicola*, and those high on dead shoots released mostly spores of *Mycosphaerella* sp. 2, or spores of *P. halima*. *Phaeosphaeria halima* was virtually absent from blades low on living shoots. *Phaeosphaeria spartinicola*, though present on the high dead blades, was a distant third in the rank of ascospore-release frequency (18% of *P. halima*). Potential reasons for this disparity between types of leaf include: (i) less exposure to saltwater during flooding tides for high blades (Newell et al., 1998); (ii) less exposure to shoot-climbing, mycophagous shredder invertebrates such as periwinkles (Graça et al., 2000); (iii) more exposure to solar irradiation at the top of the grass canopy; (iv) greater access to nutrients deposited with precipitation (Paerl et al., 1999); (v) different balance in the competition among ascomycetous decomposers (Shearer, 1995).

Spatial patchiness of rates of ascospore release is a prominent characteristic of the cordgrass-decay system. In spite of the fact that we attempted to collect blades of uniform appearance for each leaf type, and that we pooled counts for five 1-mm^2 fields for each of four replicate leaves for each wet-incubation time × site, we routinely found CVs > 100% for our mean rates of ascospore release, even for the two *Phaeosphaeria* species, with the more stable rates (Tables 1, 2). This high level of patchiness (also seen previously: Newell and Wasowski, 1995; Newell and Wall, 1998; Newell et al., 2000a, b) seems curious in an ecosystem characterized by a high degree of uniformity in vascular-plant species composition and distribution (Dardeau et al., 1992; Bertness and Pennings, 2000). Perhaps the patchiness serves to provide a steady stream of ascospores for capture of newly available substrate (newly dead leaf blades). Or perhaps we did not satisfactorily standardize our collected leaf samples; i.e., perhaps our blades were unexpectedly variable in state of decay and/or in impact of environmental variables influencing asco-

spore maturation and release such as rain, dew, tides, solar irradiation, invertebrate mycophagy (see Arseniuk et al., 1998; Graça et al., 2000; Ingold, 1971; Jailloux et al., 1999; Kurkela, 1997; Newell and Porter, 2000; Paulitz, 1996). The fact that the period without rain was not significantly correlated to ascospore-release rates suggests that at least one potentially important environmental variable was not likely to have contributed to the patchiness that we observed in mean rates. This unexplained patchiness is one indication that we have a great deal yet to learn about the controls of ascospore production and interactions among ascomycetous decomposers in smooth-cordgrass marshes. It is conceivable that improved understanding of saltmarsh-ascomycete ecology could assist in improving understanding of functioning of ascomycetes of commercially important and invasive grasses (see, e.g., Arseniuk et al., 1998; Fallah and Shearer, 1998; Halama et al., 1999; Loughman et al., 1996; Paulitz, 1996; Wong et al., 1998), especially since *S. alterniflora* itself is considered invasive in some environments (see Daehler and Strong, 1997).

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