Sphagnum Moss Disperses Spores with Vortex Rings

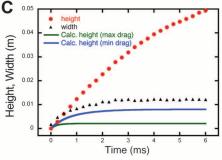
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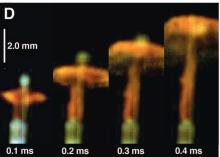
∀phagnum moss forms deep mats covering over 1.5 million km² or 1% of Earth's land surface (1) and is important in the global carbon cycle, potentially storing more carbon than any other plant genus (2). With over 285 species (3), often with specific microhabitats, long-distance spore dispersal by wind is critical in maintaining this genus (1). To travel long distances, Sphagnum spores must move through the laminar boundary layer into the turbulent boundary layer (up to 10 cm above the ground), where eddies can carry small particles upward and laterally (4). The terminal velocity of Sphagnum spores is 5 mm s $^{-1}$ (5, 6), indicating that any updraft exceeding this quantity is sufficient to hold them aloft. However, spores with low terminal velocities rapidly decelerate in still air, and dispersal range depends on release height, which is limited for this nonvascular plant. Here, we show that the mechanism Sphagnum uses to project spores to heights suitable for dispersal is the generation of turbulent vortex rings: ellipsoidal bubbles of distributed, toroidal vorticity whose internal flow fields sustain their translational motion (6)

To reach turbulent air, spores are explosively liberated. Our observations show that spores reach heights that cannot be explained by ballistic trajectories. On sunny days capsules dehydrate, and epidermal cells of the capsule body collapse laterally, causing capsules to change shape from spherical to cylindrical (Fig. 1A) and increasing the internal air pressure to between 200 and 500 kPa (7). Eventually pressure forces the cap to break free in under 10^{-5} s, vertically propelling the air and spores (Fig. 1D and movies S1 to S4) with an average launch velocity of $16 \pm 7 \text{ m s}^{-1}$ (mean \pm SEM, n = 15, range from 7.9 to 29.8 m s⁻¹) to a mean height of 114 ± 9 mm (mean \pm SEM, n = 12, range from 90 to 166 mm). These heights cannot be explained by ballistics. Spores launched ballistically with the measured initial velocity of 13 m s⁻¹ would reach a maximum height of only 2 to 7 mm in under 0.5 ms. Whereas after 5 ms, spores traveled over 40 mm while still moving at 3 m s $^{-1}$ (Fig. 1C).



Fig. 1. (**A**) *Sphagnum affine* capsule transformed from round to cylindrical. (**B**) A longitudinal section of a capsule showing spore distribution before exploding. (**C**) Trajectory of spore launch. The observed height (circles) and width (triangles) of the spore cloud versus time from video recorded at 4000 frames per s. Blue and green curves are predicted trajectories of a single spore ballistically launched through still air (*6*). (**D**) Sequential video frames of an exploding capsule recorded at 10,000 frames per s with 20-μs exposure.





High-speed videos indicate that the generation of turbulent vortex rings by exploding capsules is responsible for the continued trajectory. The sudden release of air and entrained spores from the circular capsule opening provides the cylindrically symmetric impulse required to generate vortex rings (8). The spores in the images reveal the characteristic mushroom cloud indicative of turbulent vortex rings (Fig. 1D and movies S2 and S3) (6). Spores uniformly distributed over a height of 1 mm in the capsule (Fig. 1B) are concentrated to a height of only 0.3 mm in the vortex bubble that grows to a constant width (Fig. 1C). The drag coefficient, C_D , for the vortex bubble in Fig. 1C is between 0.06 and 0.17 (6). This agrees with drag measured for vortex rings in water ($C_D = 0.09 \pm 0.01$) (9) and indicates the efficiency with which Sphagnum vortex rings travel through still air.

Vortex rings are commonly generated by animals such as jellyfish and squid for propulsion (10). Here, we report vortex rings generated by a plant. The enhanced dispersal from vortex rings explains in part the success of *Sphagnum*, a nonvascular plant that has thrived even after the appearance of land plants with the benefit of well-developed vascular systems.

References and Notes

- H. Rydin, J. Jeglum, The Biology of Peatlands (Oxford Univ. Press, Oxford, 2006).
- R. S. Clymo, P. M. Hayward, Bryophyte Ecology,
 A. J. E. Smith, Ed. (Chapman and Hall, New York, 1982).
- C. B. McQueen, R. E. Andrus, in Flora of North America North of Mexico, Flora of North America Editorial Committee, Ed. (Oxford Univ. Press, Oxford, 2007), vol. 27, pp. 45–101.
- P. H. Gregory, The Microbiology of the Atmosphere (Wiley, New York, ed. 2, 1973).
- 5. S. Sundberg, Ann. Bot. (London) 105, 291 (2010).
- Materials and methods are available as supporting material on Science Online.
- 7. S. Nawaschin, Flora 83, 151 (1897).
- 8. G. K. Batchelor, *An Introduction to Fluid Dynamics* (Cambridge Univ. Press, Cambridge, 1967).
- 9. T. Maxworthy, J. Fluid Mech. 64, 227 (1974).
- 10. J. O. Dabiri, Annu. Rev. Fluid Mech. 41, 17 (2009).
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Supporting Online Material

www.sciencemag.org/cgi/content/full/329/5990/406/DC1 Materials and Methods

Fig. S1 References Movies S1 to S4

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