

1 **Matters arising: Droplet-induced surface aeration, not acoustic**  
2 **sensing, most parsimoniously explains accelerated germination**  
3 **of submerged rice seeds**

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12 **In response to** Makris, N.C. & Navarro, C. (2026). Seeds accelerate germination at beneficial  
13 planting depths by sensing the sound of rain. *Scientific Reports*, 16, 11248.  
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16 When water drops strike the surface above submerged rice seeds, the seeds germinate  
17 faster, an effect that scales with drop height and falls off sharply with distance. Makris and  
18 Navarro<sup>1</sup> attributed this to acoustic stimulation of statoliths, specialised gravity-sensing  
19 organelles, suggesting seeds can effectively sense the sound of raindrops. Here I argue  
20 that a simpler, well-established physical mechanism offers a more compelling  
21 explanation: each drop impact stirs and renews the water surface, introducing oxygen from  
22 the air into the oxygen-depleted water surrounding the seeds. Submerged seeds operate  
23 under severe oxygen limitation, a physiological bottleneck that even modest aeration can  
24 substantially alleviate, making droplet-induced oxygen delivery a sufficient cause of the  
25 observed germination response with no need to invoke a novel sensory pathway. Critically,  
26 both explanations generate identical predictions under the experimental conditions used,  
27 so the data cannot distinguish between them. Additional concerns arise from the choice of  
28 Texmati rice, a cultivar with no known tolerance for sustained submergence, making any  
29 adaptive story around rain-sensing physiologically and ecologically difficult to justify.  
30 Targeted experiments that independently control dissolved oxygen, mechanical  
31 disturbance, and rice genotype are proposed to discriminate between the competing  
32 hypotheses.

33 Plants perceive diverse environmental cues such as shifts in light levels and spectral  
34 composition, volatile metabolites, soil chemistry, and signals from neighbours, that trigger  
35 adaptive responses to imminent challenges and opportunities. Natural selection, however,  
36 is expected to favour such responsiveness only when the perceived information reliably  
37 and predictably correlates with fitness-relevant conditions<sup>2,3</sup>.

38 Makris and Navarro<sup>1</sup> reported that Texmati rice (*Oryza sativa* L.) seeds submerged for six  
39 days germinated at substantially higher rates when a steady stream of water drops fell onto  
40 the water surface above them, with germination rate rising with drop height and declining  
41 with lateral distance. The authors attributed this effect to acoustic stimulation of statoliths  
42 (gravity-sensing organelles in statocyte cells of the seed), and proposed that this sensitivity  
43 allows seeds to perceive rain and accelerate germination at adaptively favourable shallow  
44 soil depths. The paper attracted wide media attention framed around the idea that seeds  
45 can ‘hear’ rain. Here, I critically evaluate the experimental design, physical interpretation,  
46 and biological relevance of these findings and argue that the reported effects can be more  
47 parsimoniously explained by droplet-induced aeration of the hypoxic seed environment.  
48 Decisive experiments to discriminate between the competing hypotheses are proposed.

#### 49 **Rice seeds under hypoxic stress**

50 Makris and Navarro used Texmati rice, a hybrid of American and Basmati long-grain  
51 cultivars (RiceTec, Alvin, Texas) selected for grain-quality and milling traits rather than  
52 submerged germination. Although Texmati rice has not been genotyped for anaerobic  
53 germination (AG) tolerance, large-effect quantitative trait loci (QTLs) conferring anaerobic  
54 germination capacity in flood-adapted varieties have not been identified in its parental  
55 lines<sup>4,5</sup>. Even in more tolerant rice cultivars, submerged germination imposes severe  
56 physiological stress: seed imbibition rapidly depletes the dissolved oxygen (DO) in the  
57 diffusion boundary layer, forcing metabolism into inefficient fermentation, restricting ATP

58 production, and depleting carbohydrate reserves<sup>6,7,8</sup>. Prolonged hypoxia and anoxia also  
59 cause cytoplasmic acidification and post-anoxic oxidative stress upon reoxygenation<sup>9</sup>.  
60 Accordingly, six days of continuous submergence are expected to depress germination  
61 markedly, as confirmed by Makris and Navarro's<sup>1</sup> own controls, which reached only ca. 45–  
62 60% cumulative germination by day 6, well below the  $\geq 80\%$  standard minimum  
63 recommended by the International Rice Research Institute<sup>10</sup>. Together, these observations  
64 establish that the seeds in these experiments were subjected to sustained oxygen  
65 limitation.

#### 66 **Raindrop sensing under submergence offers little benefit**

67 In many plants, seeds integrate multiple cues such as daylength, temperature, light levels  
68 and quality, moisture, and oxygen to break dormancy only under favourable conditions<sup>11</sup>.  
69 Makris and Navarro<sup>1</sup> proposed that sensing the sound of rain enables seeds to accelerate  
70 germination at shallow soil depths, where puddle submergence is transient and seedling  
71 survival is feasible. This adaptive rationale is, however, undermined at several levels. First,  
72 their experiments were conducted under sustained submergence, a condition ecologically  
73 distinct from the transient puddle scenario invoked in the adaptive argument. Second, for a  
74 dormant seed, puddle formation is itself unambiguous evidence of water abundance,  
75 rendering further acoustic confirmation redundant. Third, and most critically, in a  
76 submergence-intolerant cultivar<sup>12</sup>, accelerating germination under sustained submergence  
77 is more likely to hasten carbohydrate depletion and seedling death than to enhance fitness.  
78 An adaptive case for acoustic rain-sensing would require demonstration in ecologically  
79 relevant, flood-tolerant genotypes under conditions that match the proposed selective  
80 context.

#### 81 **The aeration hypothesis: a more parsimonious explanation**

82 When water drops impact a quiescent surface, >99.999% of their kinetic energy is  
83 dissipated into hydrodynamic flow and turbulence<sup>13</sup>. This process enhances dissolved  
84 oxygen (DO) at the seed surface via two non-mutually exclusive mechanisms. (i) *Surface*  
85 *renewal*: each impact intermittently disrupts the stagnant diffusion boundary layer at the  
86 air–water interface, exposing oxygen-deficient water to the atmosphere where it absorbs  
87 oxygen. The oxygen transfer rate is governed by Higbie’s surface-renewal theory<sup>14</sup> and  
88 increases with drop height, consistent with enhanced interfacial renewal and reduced  
89 liquid-side mass-transfer resistance<sup>15</sup>. Using the Chern & Yang<sup>15</sup> model for oxygen transfer  
90 in hydraulic drop structures as an order-of-magnitude guide (assuming a typical oxygen  
91 saturation deficit of ~100–200  $\mu\text{mol L}^{-1}$  and a 3.5 cm impact radius<sup>1</sup>), a single 4.7 mm  
92 diameter drop falling from 2.1 m is estimated to deliver a DO pulse of ~0.1–0.5  $\mu\text{mol L}^{-1}$  per  
93 drop within the impact zone. For comparison, ~200 imbibing rice seeds consume  
94 approximately 60–200  $\text{nmol O}_2 \text{ s}^{-1}$  in aggregate<sup>8</sup>. At one drop per 2.5–3.5 s, the cumulative  
95 aeration rate is plausibly comparable to seed oxygen demand. Under continuous dropping,  
96 the system reaches steady state where  $\text{O}_2$  input balances seed consumption,  
97 continuously alleviating the severe hypoxia expected in the no-drop controls. Note that the  
98 Chern & Yang model was developed for hydraulic drop structures rather than single  
99 impulsive drops in small basins; this estimate is therefore indicative rather than definitive,  
100 and direct measurements of DO dynamics in the experimental system are needed. (ii)  
101 *Falling-droplet interfacial gas exchange*: falling drops equilibrate partially with atmospheric  
102  $\text{O}_2$  during descent, delivering slightly oxygen-enriched water to the basin<sup>16</sup>. Higinio et al.<sup>17</sup>  
103 showed directly that raindrop pressure fluctuations enhance oxygen exchange at the  
104 water–sediment interface in shallow water, with increased sediment DO consumption  
105 consistent with elevated DO delivery from the surface, directly supporting the physical  
106 plausibility of the aeration mechanism proposed here. Both processes are well-established  
107 and require no novel assumptions.

108 Moreover, the spatial pattern of germination enhancement reported by Makris & Navarro<sup>1</sup>,  
109 with the largest effects directly below the impact point, declining significantly at ~5 cm, and  
110 no significant effect at ~20 cm, is consistent with both the acoustic-mechanical hypothesis  
111 of Makris & Navarro and the aeration hypothesis presented here. Both mechanisms predict  
112 a steep decay of effect with radial distance from the impact epicentre: near-field acoustic  
113 forcing on seeds diminishes rapidly with distance from the source<sup>1</sup>, and turbulence-driven  
114 dissolved oxygen enhancement from drop impacts similarly decays over centimetre scales  
115 away from the impact zone<sup>18</sup>. Spatial data alone therefore cannot discriminate between the  
116 two hypotheses; concurrent dissolved oxygen measurements, or experiments under  
117 controlled hypoxic or hyperoxic conditions, would be required to do so.

### 118 **Decisive experiments**

119 Both hypotheses generate identical observational predictions under the Makris & Navarro<sup>1</sup>  
120 design, but diverge sharply in their mechanistic predictions. The following are two  
121 conceptual experimental designs that would discriminate between the acoustic and the  
122 aeration hypotheses.

123 *Experiment 1: Factorial drops x DO x genotype.* Germination rate is recorded in a three-way  
124 factorial design crossing drop exposure (drops vs. no drops), dissolved oxygen level  
125 (normoxia vs. hypoxia, controlled by N<sub>2</sub> sparging or a DO-stat controller), and rice variety  
126 (submergence-susceptible, e.g. Texmati, vs. submergence-tolerant, e.g. a Sub1A or AG-  
127 QTL variety). The aeration hypothesis predicts a significant Drops x DO x Variety interaction,  
128 with the drops effect confined to hypoxic conditions and submergence-susceptible  
129 varieties. The acoustic hypothesis predicts a positive drop effect regardless of DO level and  
130 variety.

131 *Experiment 2: Acoustic exposure without hydrodynamic perturbation.* Submerged seeds  
132 are exposed to synthesized acoustic signals at 10–100 Hz and amplitudes matching those

133 measured by Makris and Navarro<sup>1</sup>, delivered via an underwater speaker positioned at  
134 sufficient distance to produce the target pressure at seed level while minimising near-field  
135 hydrodynamic flow from the speaker membrane. If acoustic exposure alone accelerates  
136 germination regardless of DO level, the acoustic hypothesis is supported. Absence of an  
137 effect under controlled DO and without surface disruption would strongly support the  
138 aeration hypothesis. It should be noted, however, that a positive acoustic result would not,  
139 in itself, validate the statolith model<sup>1</sup> and would require further mechanistic investigation.

#### 140 **Discussion**

141 Makris and Navarro<sup>1</sup> report that submerged rice seeds germinate faster under water-drop  
142 exposure, with the effect scaling with drop height and decaying with lateral distance, a  
143 result that is internally consistent and merits rigorous follow-up. Their proposed  
144 mechanism and adaptive rationale, however, are considerably less convincing and more  
145 parsimoniously accounted for by a simpler framework.

146 The statolith-acoustic hypothesis rests on a causal chain linking drop impact to statolith  
147 displacement and accelerated germination. A critical premise of this chain is that the  
148 hydrophone-recorded signal is predominantly acoustic. As demonstrated above, the  
149 pressure measured at 1–2 cm from a drop impact in a 3 cm basin at 10–100 Hz is  
150 dominated by near-field hydrodynamic motion; the acoustic fraction carries at most ca.  
151  $10^{-5}$  of total drop kinetic energy<sup>13,19</sup>. Direct imaging of statolith displacement in rice embryos  
152 at the measured pressure amplitudes is not provided, nor is it demonstrated that the net  
153 pressure amplitude is sufficient to trigger a sensory cascade. Rice statoliths are  
154 established mediators of gravitropism<sup>21,22</sup>, but their proposed function as acoustic  
155 transducers tuned to raindrop frequencies is merely speculative and lacks direct biological  
156 support.

157 In contrast, the aeration hypothesis rests entirely on established hypoxic-stress  
158 physiology<sup>6,7,8,9</sup>, surface-renewal gas-transfer theory<sup>14</sup>, well-characterised oxygen-demand  
159 dynamics during imbibition, and direct empirical evidence that raindrop pressure  
160 fluctuations enhance sediment DO in shallow water<sup>17</sup>. When two hypotheses are  
161 observationally indistinguishable, parsimony serves as a pragmatic epistemic heuristic  
162 favouring the model with fewer unverified assumptions<sup>22</sup>. The asymmetry here is stark: the  
163 aeration framework requires only established physiology and known gas-transfer physics,  
164 whereas the acoustic-stalolith framework requires a novel transduction mechanism at  
165 ultra-low near-field pressures, a multifunctional use of the gravitropic pathway, and an  
166 adaptive rationale that is difficult to reconcile with the sustained submergence conditions  
167 and submergence-intolerant genotype used.

## 168 **Conclusion**

169 The findings reported by Makris and Navarro<sup>1</sup> generate a mechanistically rich question  
170 worth pursuing. The true value of an ambitious hypothesis, however, lies in how it  
171 withstands careful scrutiny, not in its rhetorical appeal. Experimental design is not a  
172 technical afterthought but the epistemic backbone of scientific inference: it must separate  
173 proposed causes from plausible alternatives, control confounding variables explicitly, and  
174 preserve a defensible chain from observation to mechanism. Without such a framework,  
175 interpretation may outrun inference, and an attractive narrative can masquerade as  
176 mechanistic explanation.

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239 **Declaration of generative AI and AI-assisted technologies**

240 During the preparation of this work, I used Perplexity Pro to improve the wording and for  
241 proofreading. After using this tool, I reviewed and edited the content, and I take full  
242 responsibility for the content of the published article.