



Spatial resource arrangement influences both network structures and activity of fungal mycelia: A form of pattern recognition?

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ABSTRACT

The present study investigated the behavior and wood decay ability of mycelial network of *Phanerochaete velutina*, a cord-forming fungus, on multiple wood blocks. We placed well-colonized wood blocks in two spatial arrangements (Circle and Cross) on a soil plate and compared the development of the mycelial network and wood decay over 116 days. In the Circle arrangement, the degree of connection (number of connected cords) of the blocks ranged from 0 to 8, with no significant differences observed across positions. However, in the Cross arrangement, the outer blocks exhibited a greater degree of connection than the inner blocks. The mass loss of the wood block was positively associated with the degree of connection and was significantly smaller in the Cross than in the Circle arrangement. These findings suggest that fungal mycelium can “recognize” the difference in the spatial arrangement of wood blocks as part of their wood decay activity.

1. Introduction

Cognitive behavior, such as learning, decision-making, problem-solving, and anticipation in organisms without a brain or central nervous system is garnering increasing attention (Lyon et al., 2021; Reid, 2023). The development of this research field has the potential to enhance our understanding of the various essential scientific topics, such as biotic ecosystem functions and the evolution of cognitive systems across organisms, as well as inspire new ideas for bio-based computing systems (Solé et al., 2019). However, previous studies have predominantly focused on plants (Plantae Trewavas, 2015) and slime molds (Animalia Dussutour et al., 2010), with fewer investigations into fungi (Fungal), which is the third and least explored kingdom of eukaryotes (Alekkett and Boddy 2021).

Several typical behaviors have been studied to evaluate cognition of organisms. In particular, finding the shortest pathway connecting multiple locations is a “cognitive toolkit” that enhances an organism’s problem-solving ability for successful survival and reproduction (Reid, 2023). The behavior of plasmodial slime molds, organisms without a brain and nervous system, has been intensively studied in this context (Reid, 2023). In a landmark study on the behavior of a model species, *Physarum polycephalum*, in a maze, Nakagaki et al. (2000) found that the

plasmodia identified the shortest path between the start and end of the maze where the food sources (baits) were deposited. Even in the case where more than two baits were provided, the plasmodia connected multiple baits via the shortest path, including both the mathematically shortest route, known as Steiner’s minimum tree, as well as other options with more robust patterns (Nakagaki et al., 2004). Furthermore, the plasmodia can optimize their network to meet the two independent and conflicting attributes to simultaneously maximize network efficiency and minimize damage from harmful stresses (Nakagaki et al., 2007). As a consequence, plasmodia can create networks that have efficiency, robustness, and costs that are comparable with the existing real railway network (Tero et al., 2010). This evidence led to a formal framework called “basal cognition” for reframing the definition of cognition as “fundamental processes, such as memory, learning, decision-making, and anticipation, and mechanisms that enabled organisms to track some environmental states and act appropriately to ensure survival and reproduction” which existed long before nervous systems evolved (Lyon et al., 2021; Reid, 2023).

On the contrary, recent studies considering neuroscience hypothesize that the cognition of humans, as a brained animal, emerges from the patterns of interconnections and information transfer across numerous neurons (Park and Friston 2013). Each neuron is a single cell with

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spreading dendritic branches that create connections with other neurons via synaptic terminals to form massive networks. The number and strength of synaptic connections are plastic and can be modified by the experiences of the neuron through cellular mechanisms that mediate short-term habituation (Kandel et al., 2013). In this context, the brain exhibits at least two levels of cognition. One is the basal cognition at the cellular level of each neuron, and the other is the classical means of cognition, which emerges from the activities and interconnections of the neural networks. This classical cognition is crucial for brained organisms to “recognize” the external world. For example, visual perception is an important aspect of the brain’s cognitive processes. When recognizing different figure images, distinct modules of neural networks in the visual cortex are activated (Tsunoda et al., 2001; Srinath et al., 2021). Therefore, “differential network activation” in the brain underpins the recognition of various figure images. In other words, if a network composed of numerous interacting units, such as cells, exhibits differential activities and information flows in response to different figure images, it could be considered “recognition”, even in a neural network. This concept is foundational to image processing in artificial intelligence (Emambocus et al., 2023; Xu et al., 2023) and decision-making in the collective behavior of animal swarms when selecting among spatially distributed options, such as food sources (Perna et al., 2012; Mann 2018). However, this concept has been underexplored in the context of “recognition” in microorganisms.

The mycelium of cord-forming wood decay fungi, which is multicellular but has a superficially similar networking body design as slime molds, grows in the soil–litter interface on the forest floor and forages for deadwood material. The mycelial network sometimes spreads over a large spatial scale of more than 900 ha (Ferguson et al., 2003). These fungi play a crucial role in the decomposition of deadwood, thereby influencing carbon and material cycling in forest ecosystems (Rayner and Boddy 1988). Previous studies have reported the intelligent behavior of mycelium, including decision-making based on nutrient status and memory of past experiences (Donnelly and Boddy 1998; Fukasawa et al., 2020; Fukasawa and Kaga 2021; Fukasawa and Ishii 2023), and even solving mazes (Held et al., 2011). Donnelly and Boddy (1998) reported that the mycelium of a wood decay basidiomycete, *Phanerochaete velutina*, experienced a partial disturbance in its network, ceased hyphal growth from the disturbed part of the mycelium, and allocated biomass to the undisturbed part after a second disturbance, indicating decision-making based on the memory of past disturbances. Similarly, researchers have found that the mycelium of *P. velutina* retains a memory of the direction to wood bait and can decide whether to migrate to new bait depending on its size, timing, and distance (Fukasawa et al., 2020; Fukasawa and Kaga 2021; Fukasawa and Ishii 2023). These behaviors in fungal mycelia are not centrally controlled but emerge from the collective behaviors of numerous hyphal tips, each sensing environmental conditions, interacting, and networking with one another (Held et al., 2019; Wernet et al., 2023; Fukasawa et al., 2024a).

Drawing an analogy to neurons and the brain discussed earlier, we hypothesized that fungal mycelium possesses cellular-level cognition at the hyphal tip, referred to as basal cognition (Lyon et al., 2021) or minimal cognition (Smith-Ferguson and Beekman 2019). In addition, we suggest that “recognition” occurs at the level of the entire mycelial body, emerging from the networked interactions of numerous hyphal tips within the mycelial network. The mycelia of wood decay fungi may serve as potential subjects to evaluate the difference in activity between different networks because of their networking nature, and with activity measurable by the mass loss of wood resources. However, the decay rate of wood by fungi has rarely been measured in studies on mycelial behavior, and no significant differences have been reported across distributions of multiple wood baits (Hughes and Boddy 1996).

In this study, we demonstrate the development of the fungal mycelium network structure connecting multiple wood blocks and its associated wood decay activities. To explore the relationship between mycelial network topology and wood decay rate, we prepared two

spatial arrangements (Circle and Cross; Fig. 1) using nine wood blocks, each colonized by a cord-forming wood decay fungus, *P. velutina*, on a soil dish microcosm. This fungus, commonly used in studies of fungal behavior (Boddy 1993, 1999; Boddy et al., 2009), has been reported to exhibit memory, learning, and decision-making abilities (Donnelly and Boddy 1998; Fukasawa et al., 2020). The Circle and Cross arrangements of the nine wood blocks were selected for comparison because they yield several different network indices if all blocks are connected to their nearest neighbors by hyphal cords (Fig. 1). Link length (total length of links in the network), mean degree (mean number of links connected to the blocks), and mean link length (mean length of the shortest link between any pairs of two blocks) are all larger in the Circle than in the Cross arrangement. We predict that (1) the wood decay rate will be higher in the Circle arrangement compared to the Cross because of the greater biomass cost for the fungus in the Circle, as indicated by the larger link length, mean degree, and mean link length. Additionally, we predict that (2) the wood decay rate will be uniform across the wood block positions in the Circle arrangement but will vary among the wood block positions in the Cross arrangement because of the differences in their degree of connected hyphal links. If a higher degree of connections allows the fungus in the wood to collect more nutrients and water via the connected hyphae, the wood decay rate at the center of the Cross might be greater than that of the outer wood blocks.

2. Materials and methods

We prepared beech wood blocks (1 × 1 × 1 cm) that were weighed after drying at 70 °C for two weeks. The weighed blocks were soaked overnight in autoclaved deionized water and incubated with *P. velutina* on 0.5% malt extract agar plates for 42 days at 20 °C in the dark. We placed the well-colonized wood blocks onto non-sterilized, moistened soil plates that were prepared in a square dish (24 × 24 cm) (Fukasawa et al., 2020). The thickness of soil was approximately 5 mm in average. Nine wood blocks were placed in a dish in a Circle or Cross arrangement, with 10 replicates each (Fig. 2). The distance between the nearest two wood blocks was standardized at 5 cm for both arrangements. The soil dishes were incubated for 116 days at 20 °C in the dark. During the incubation period, the dishes were photographed every month using a Canon EOS Kiss X5 camera (Canon, Tokyo, Japan) mounted on a stand at a height of 46 cm. The dishes were moistened every week by spraying with autoclaved deionized water and randomly repositioned to avoid the possible effect of orientation and location within the incubator on hyphal growth.

Images were analyzed using ImageJ (National Institute of Health, USA). The edge of the soil tray and wood blocks were removed, and the resulting image was converted to black and white binary using a manually set threshold to measure the hyphal coverage on the soil. Hyphal coverage was compared between the Circle and Cross arrangements at each photographing time point using the Wilcoxon rank-sum test with Bonferroni correction of the probability values.

After the incubation period, the wood blocks were harvested, dried at 70 °C for two weeks, and then weighed. The mass loss of each wood block after 158 days (42 days of colonization on agar plus 116 days of incubation on soil) was calculated as a percentage of the block’s original dry weight. The number of hyphal cords attached to each block was recorded as the degree of connection from the photographs of the mycelial network at day 116 on the soil. The data variance in the degree of connection was compared between the Circle and Cross arrangements using the Bartlett test. The mean degree of connection was compared between the Circle and Cross arrangements using the Wilcoxon rank-sum test. The mean degree of connection was also compared across the location within each arrangement using Steel-Dwass test. The relationship between the degree of connection and mass loss of the blocks in the different arrangements was analyzed using a generalized linear mixed model (GLMM), which included mass loss as a dependent variable and the degree of connection and arrangement (Circle and Cross) as

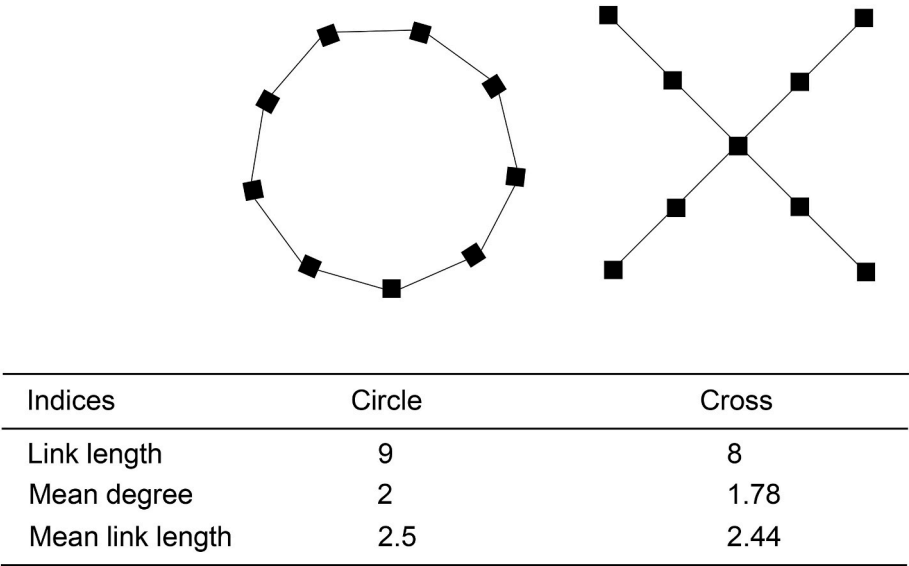


Fig. 1. Hypothetical scheme of mycelial networks for the Circle and Cross arrangements of nine wood blocks and their network indices. Black squares represent the wood block locations. Solid lines represent the predicted fungal mycelial cord connections.

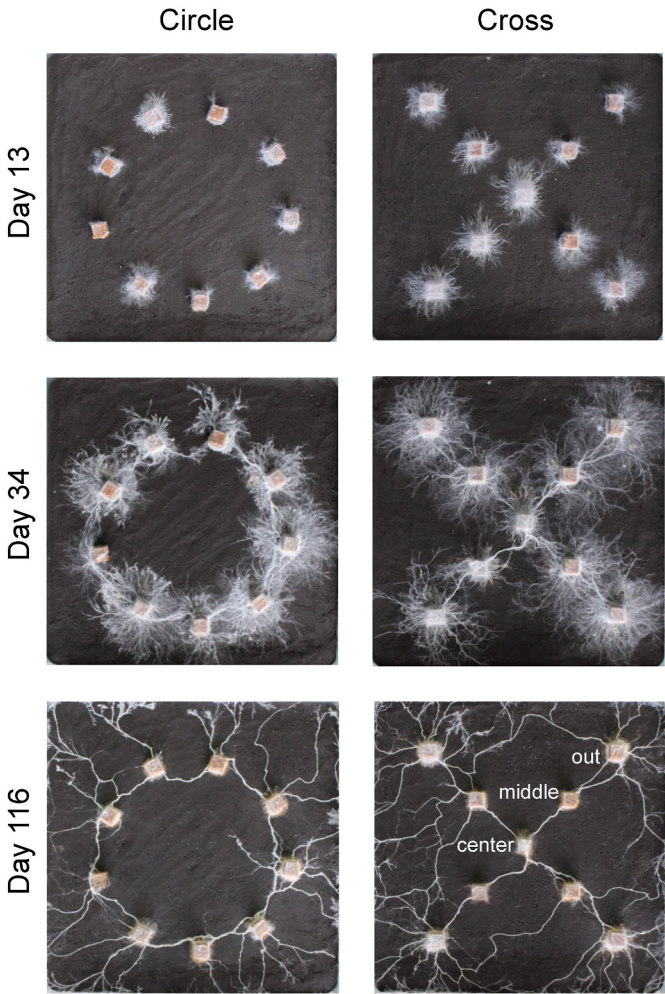


Fig. 2. The hyphal cord network of *Phanerochaete velutina* developed on the soil dish for the Circle and Cross arrangements of the wood blocks after incubation for 13, 34, and 116 days at 20 °C in the dark.

explanatory variables. The dish ID among a total of 20 soil dishes (10 replicates for each Circle and Cross arrangement) was set as a random effect. Gaussian data distribution (identity link) was assumed. In addition, we evaluated another GLMM without data from both extreme ends of the degree of connection (0 and 9) to investigate the stability of the results after removing the extreme data.

All statistical tests were performed using R 4.3.1 (R Core Team, 2023).

3. Results

During the incubation period, the hyphal coverage in the soil increased until day 34 and decreased thereafter (Fig. 3). The difference in hyphal coverage between the Circle and Cross arrangements was not significant at all the tested time points. After incubation for 116 days on the soil dish, the nine wood blocks in each dish were found to be connected by a *P. velutina* hyphal network (Fig. 2). In the Circle arrangement, the degree of connection of the nine blocks ranged from 0 to 8, and they were not significantly different across the locations within the network (Steel-Dwass test, $p = 0.127$). In the Cross arrangement, the

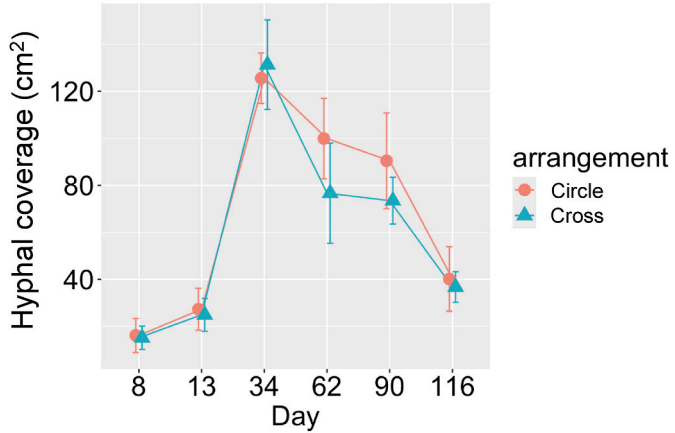


Fig. 3. Hyphal coverage (cm²) on the soil dish for the Circle and Cross arrangements during the incubation period. There were no significant differences in the hyphal coverage between the Circle and Cross arrangements at any time point tested (Wilcoxon rank-sum test, $p > 0.0083$, Bonferroni-adjusted p value).

degree of connection of the wood blocks ranged from 0 to 9, and the outer four blocks had a greater number of degrees of connection than the middle and center blocks (Steel-Dwass test, $p < 0.001$). The data variance in the degree of connection was greater in the Cross arrangement than in the Circle arrangement (Bartlett test, $p < 0.001$). The mean degree of connection was not significantly different between the Circle and Cross arrangements (Wilcoxon rank-sum test, $p > 0.05$). The mass loss of the wood blocks ranged from 18.0% to 65.5% in the Circle and from 16.7% to 62.7% in the Cross arrangement. A GLMM indicated that the mass loss of the wood blocks was positively associated with the degree of connection of the wood blocks and was significantly smaller in the Cross than in the Circle arrangement (Fig. 4, Table 1). However, if the data from both extreme ends of the degree of connection (0 and 9) were removed from the analysis, only the degree of connection was positively associated with the mass loss of the blocks, and the effect of the difference in spatial arrangement became non-significant (Table 2). The interactive effect of the degree of connection and wood arrangement on the mass loss of the blocks was not significant ($p = 0.28$) and thus not included in the model.

4. Discussion

The difference in the arrangement of the wood block locations affected the network topology of the fungal mycelium, which characterizes the material acquisition and transfer efficiency of the mycelium (Aguilar-Trigueros et al., 2022). Even starting with an evenly distributed radial hyphal extension from each wood block, the hyphal network development was obviously different across the wood blocks in the Cross arrangement after mycelial fusion. The outermost blocks had a greater degree of connection than the blocks at the center or middle of the dishes. This is opposite to our prediction (2) that the wood block at the center of the Cross arrangement would exhibit the greatest degree of connection. Nevertheless, the result is consistent with the growth polarity of the fungal mycelium. It is known that the fungal mycelium has acropetal (from the center outward) growth polarity, a phenomenon often observed in the expansion of fairy rings, which increase in diameter each year (Dowson et al., 1989). Initially, the mycelia grew outward from each block, displaying radial growth in all directions before fusing to form one large mycelium. Therefore, the results of the present study suggest that hyphal growth polarity may change following the fusion of multiple colonies. It is known that the fungal mycelium has an

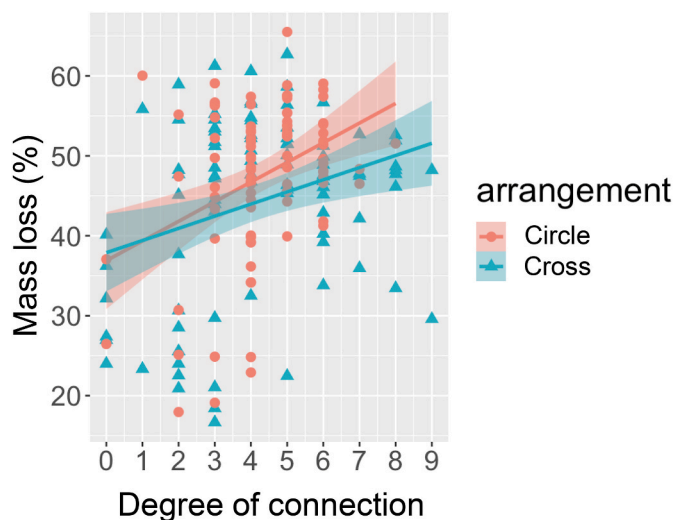


Fig. 4. The relationship between the degree of connection (number of mycelial cord connections) and mass loss (%) of the wood blocks in the Circle and Cross arrangements after the incubation period. The lines represent regression lines with 95% confidence intervals.

Table 1

Results of GLMM explaining relationships between mass loss of wood blocks and their degree and spatial arrangement.

Factors	Estimate	SE	df	t	p
degree	1.79	0.3962	177	4.529	<0.0001
arrangement (Cross)	−3.04	1.4831	177	−2.049	0.042

Table 2

Results of GLMM without data of extreme degree of connection (0 and 9) explaining relationships between mass loss of wood blocks and their degree and spatial arrangement.

Factors	Estimate	SE	df	t	p
degree	1.58	0.4736	167	3.344	0.00102
arrangement (CROSS)	−2.47	1.5174	167	−1.627	0.10572

oscillation rhythm of calcium ion concentration at the hyphal tip (Takeshita et al., 2017) as well as oscillations in material transfer and electrical activity within the mycelial body (Fricker et al., 2007; Fukasawa et al., 2024a). After fusion, these oscillations in multiple hyphae and colonies tend to synchronize (Fricker et al., 2009; Wernet et al., 2023). This suggests that fungal mycelia may be capable of processing information about spatial locations within their network and adaptively altering their behavior, possibly by synchronizing their oscillations, similar to what has been observed in slime molds (Boussard et al., 2021).

Given the positive correlation between the degree of connection and wood decay rate, the blocks in the Cross arrangement were well-distinguished within the mycelial network. Therefore, our prediction (2), that the decay rate of the blocks would differ based on their positions in the Cross arrangement due to variations in their degree of connection, was partially supported. The outermost four blocks, which had a greater degree of connection, may have served as “outposts” for foraging and absorbing water and nutrients from the soil, facilitated by their greater hyphal connections. Water and nutrient transfer through the hyphae are crucial for decomposing organic materials in a heterogeneous environment (Boswell et al., 2002; Boberg et al., 2014; Guhr et al., 2015; Fukasawa et al., 2024b). In contrast, the inner five blocks, with fewer hyphal connections, likely supported material transport and possibly became a “pathway” for the hyphal cords rather than absorbing water and nutrients. Some blocks were abandoned (0 degrees of connection) to maximize network efficiency (Fricker et al., 2017). Although the photographic images did not capture the distribution of the mycelium within the soil, it is unlikely that significant mycelium was present in the areas where hyphal coverage was not visible, as the mycelial cords were attached to the wood blocks and easily peeled off from the soil when we harvested them, without disturbing the soil surface.

As predicted, these topological differences across the blocks were not observed in the Circle arrangement. Although the degree of connections varied and an associated variation in the decay rate was observed, these variations appeared random and did not correspond to any particular position within the Circle. Interestingly, after the hyphae fused and grew outward from the nine wood blocks, a sparse hyphal distribution was observed in the interior area of the dishes in the Circle arrangement, indicating a change in growth polarity, as previously discussed. By day 34 (Fig. 2), when hyphal coverage was its maximum during the incubation period (Fig. 3), a large empty area without hyphae had formed at the center of the dishes with the Circle arrangement. This suggests that the fused mycelium altered its growth polarity without occupying the “center” of the newly fused large mycelium. It is unclear how the fused mycelium identified its new “center” after fusion. Possibly, the increased hyphal density within the Circle negatively affected growth in that area, causing it to cease. Previous studies have shown that mycelium growth stops when hyphal density per unit surface area exceeds a certain

maximum (Trinci 1974). Given that the tray lid was loosely placed and opened weekly to spray water evenly on the soil surface, we believe the oxygen level was not low at the center of the tray. Nevertheless, it would be valuable to investigate whether this phenomenon occurs in an experiment without a lid.

Although affected by some outlier data, the Circle and Cross arrangements did indeed alter the wood decay activity of the fungal mycelia, supporting our prediction (1). Previous studies have shown that wood decomposition by *P. velutina* is highly correlated with its hyphal growth on soil (Fukasawa and Kaga 2020). However, in this study, no significant difference in hyphal coverage was observed between the Circle and Cross arrangements at any time point. This suggests that the wood decay activity of *P. velutina* mycelia was not associated with the production cost of the mycelium, but rather with differences in the mycelial network structure resulting from the spatial distribution of the wood blocks. This is analogous to the way different visual images activate distinct neuron networks in the visual cortex, enabling the brain to recognize different images (Tsunoda et al., 2001; Srinath et al., 2021). Whether or not mycelium is conscious is irrelevant in this context, as cognitive processes function independently of consciousness, even in the brain (Kandel et al., 2013). If we define cognition as “the sensory and information-processing function of autonomous biological systems (Lyon et al., 2021),” the difference in network structure and wood decay function that was demonstrated by the fungal mycelia between the Circle and Cross arrangements might be a form of recognition by fungi. The functional significance of the fungal mycelia may provide insights into studying the primitive intelligence of brainless organisms (Money 2021), understanding its ecological impacts (Alekklett and Boddy 2021), and developing bio-based computers (Adamatzky 2023).

Data availability

The data presented in this study are available on request from the corresponding author.

CRedit authorship contribution statement

Yu Fukasawa: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kosuke Hamano:** Methodology. **Koji Kaga:** Methodology. **Daisuke Akai:** Methodology. **Takayuki Takehi:** Methodology.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Experimental research and field studies on fungi including the collection of fungal material, are complied with relevant institutional, national, and international guidelines and legislation.

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