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Authors

Treseder, Kathleen K
Schimel, Joshua P
Garcia, Maria O
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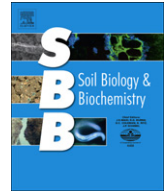
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Short Communication

Slow turnover and production of fungal hyphae during a Californian dry season

Kathleen K. Treseder^{a,*}, Joshua P. Schimel^b, Maria O. Garcia^a, Matthew D. Whiteside^a^a Department of Ecology and Evolutionary Biology, University of California, 361 Steinhaus Hall, Irvine CA 92697, USA^b Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA

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ABSTRACT

We used minirhizotrons to examine the production and turnover of fungal hyphae *in situ* during the dry season in a Californian grassland. Hyphae were produced relatively slowly throughout the season at rates that did not vary significantly over time, indicating that a portion of the fungal community was active even when soils were very dry. In addition, fungi displayed relatively long residence times, with half of the hyphae remaining in the soil for at least 145 days. Together, these results suggest that a contingent of active fungi may be capable of performing nutrient transformations when plants are otherwise dormant, while relatively long-lasting hyphae may immobilize nutrients for several months before turning over.

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Microbes can serve as mechanisms of nutrient retention within ecosystems during the “non-growing seasons” of plants, especially if microbial turnover is low during these periods (Singh et al., 1989; Vitousek and Matson, 1984). In Mediterranean climates, for example, summers are dry, and many plants die or are drought-deciduous. Even so, microbial biomass can increase or remain relatively stable during this time (Vourlitis et al., 2009). In addition, microbial processes such as heterotrophic respiration and denitrification can respond very quickly (within hours) to moisture pulses during dry seasons in Mediterranean systems (Xu and Baldocchi, 2004) and elsewhere (Davidson et al., 1993), indicating that populations of viable microbes are maintained during this period. Nevertheless, studies of microbial dynamics tend to focus on the growing seasons of plants (Wardle, 1998).

Moreover, as microbes die and decompose, their component nutrients can be acquired by other organisms, released into the atmosphere as trace gases, or leached from soils (Chapin et al., 2002). Thus, turnover rates of microbes (including fungal hyphae) can influence the loss and retention of C and N in soils (Schmidt et al., 2007; Singh et al., 1989; Vitousek and Matson, 1984). Population dynamics can also control shifts in microbial community composition in response to environmental change

(Allison and Martiny, 2008; Schmidt et al., 2007; Wardle, 1998; Zak et al., 1995). A significant portion of the microbial community is composed of fungi (Fierer et al., 2009). Previous studies have reported that single fungal hyphae turnover rapidly—on the order of two weeks or less (Atkinson and Watson, 2000; Bago et al., 1998; de Vries et al., 2009; Friese and Allen, 1991; Staddon et al., 2003a). However, field-based studies are rare, with the exception of a soil biotron study in a mixed-hardwood forest in Michigan (Atkinson and Watson, 2000).

We used minirhizotrons in an annual grassland in the University of California Sedgwick Reserve in central California to determine *in situ* rates of turnover, production, and disappearance of individual fungal hyphae during the dry season (Fig. 1). This ecosystem experiences a Mediterranean climate with hot, dry summers and cool, moist winters (Fig. 2a). Hyphal production was estimated by noting the first appearance of individual structures; and decomposition, by disappearance. In addition, standing hyphal counts were determined for each minirhizotron tube. Altogether, 149 hyphae were each visible on at least two dates during the sampling period; we were able to calculate lower-bound estimates of residence times for each of these hyphae. Some, but not all, of these hyphae were attached to plant roots and displayed angular branching typical of arbuscular mycorrhizal (AM) fungi. The AM hyphae, especially, may be either dead or dormant, since most host plants were not active during the sampling period.

* Corresponding author. Tel.: +1 949 824 7634; fax: +1 949 824 2181.

E-mail address: treseder@uci.edu (K.K. Treseder).

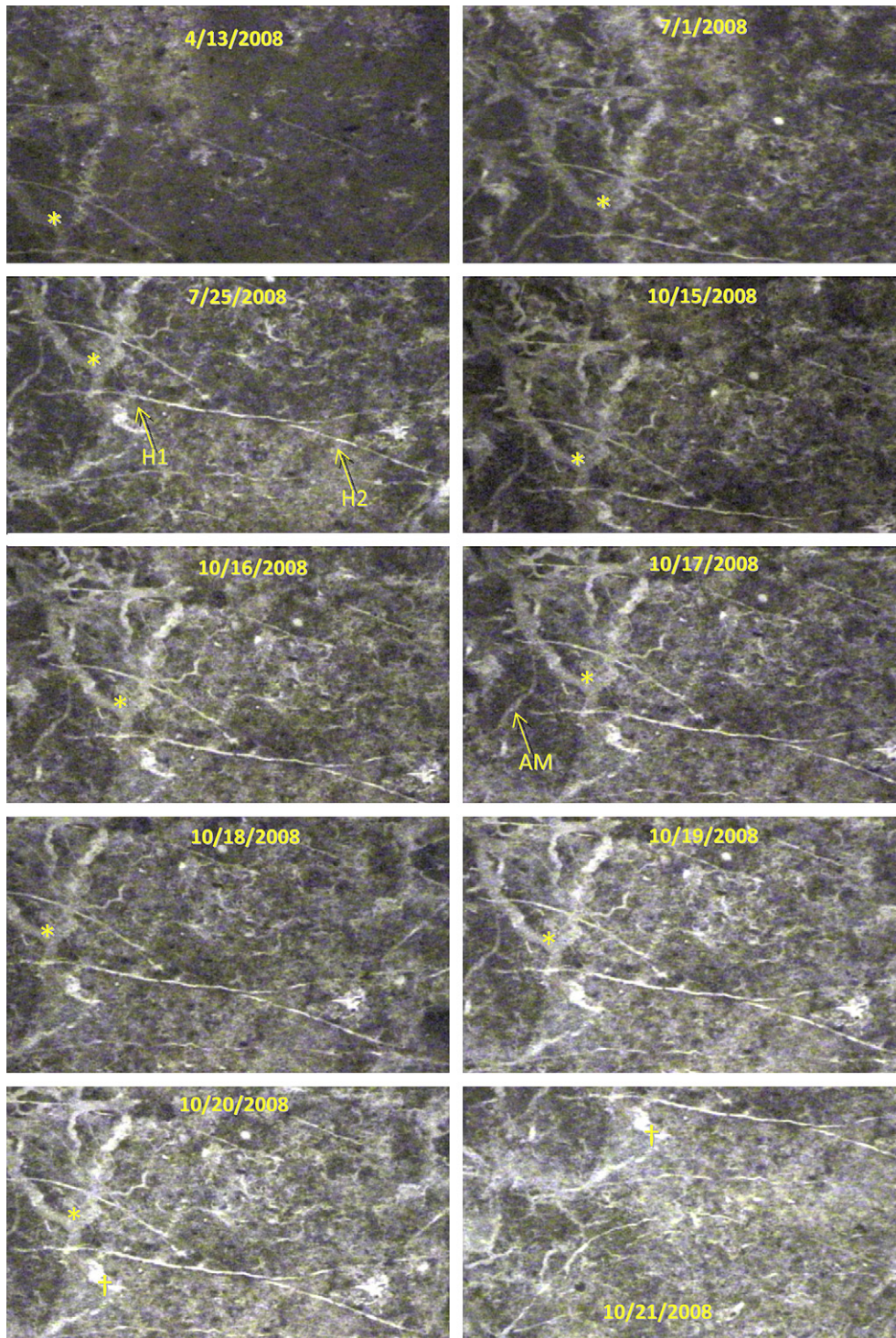


Fig. 1. Sequential frames recorded in a minirhizotron installed in the Sedgwick Reserve, California USA (34° 42'30"N, 120° 2'30"W). To determine fungal turnover, we examined sequences of hyphal images such as these. Numbers designate sampling date. We georeferenced prominent structures (e.g., aggregates and roots) in the images to align sequential recordings. A given hypha was only categorized as absent if its expected location (based on images from other dates) was recorded and the hypha was not visible. In this sequence, the asterisk (*) indicates a root section used as a georeference point for dates 4/1/08 to 10/20/08; the dagger (†), a georeference point between dates 10/20/08 and 10/21/08. The hypha H1 could be confirmed as present for dates 4/1/08 through 10/21/08, with a calculated residence time of at least 202 days. The hypha H2 could be confirmed as present on dates 7/25/08 through 10/21/08, for a residence time of at least 88 days. The hypha marked "AM" is putatively an arbuscular mycorrhizal hypha, given its connection with a fine root. In this particular frame, no hypha was categorized as growing or as disappearing over the sampling period. Most hyphae (>95%) were hyaline. Hyphal diameter ranged from 0.4 to 5.2 μm . In this site, the invasive grasses *Bromus diandrus*, *Bromus hordaceus*, and *Avena fatua* were dominant. These genera are AM hosts (Rillig et al., 1998). In April 2007, we installed 16 clear plastic 1-m long, 5-cm diameter minirhizotron tubes at 45° angles to the soil surface in three blocks of the grassland spanning 1 ha. Observations were made along the entire length of each tube (0–0.7 m soil depth). The soil area represented in each image was $0.27 \times 0.20 \text{ cm}^2$, and an average of 13 images were collected along each tube at each date. We used a minirhizotron camera (BTC-100X, Bartz Technology, Santa Barbara, CA) to record images of mycorrhizal structures visible from the tubes on 4/13/08, 4/30/08, 5/29/08, 6/30/08, 7/25/08, 10/15/08, 10/16/08, 10/17/08, 10/18/08, 10/19/08, 10/20/08, and 10/21/08. This model of minirhizotron camera is equipped with 100 \times magnification, and single hyphae are visible at these magnification levels. The intensive sampling period during October was used to capture any high-resolution hyphal dynamics under particularly dry conditions.

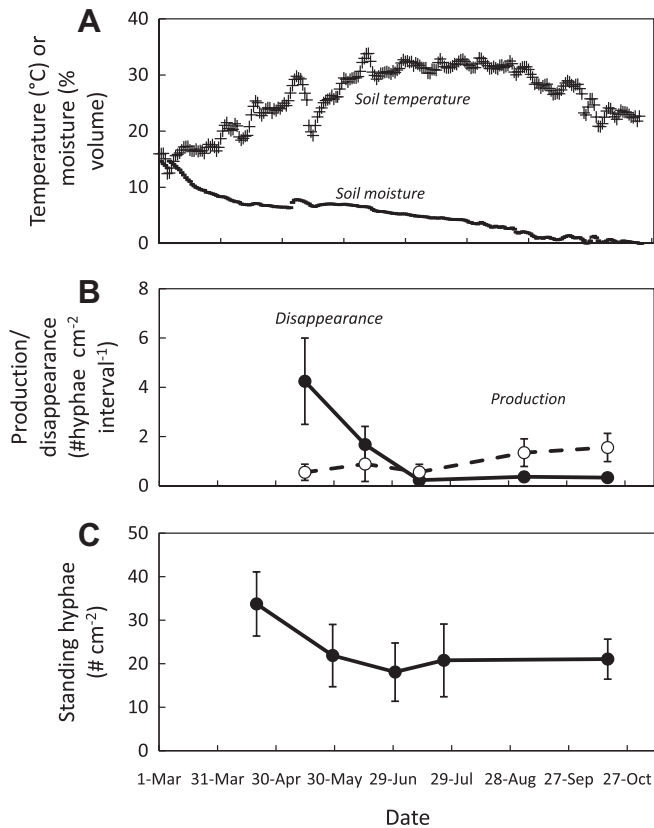


Fig. 2. Average daily soil temperature and soil moisture at 15 cm depth in Sedgwick Reserve during 2008 (data courtesy <http://www.geog.ucsb.edu/ideas/>) (A), rates of disappearance and production of hyphae (B), and standing hyphal length (C). Annual rainfall averaged 380 mm y^{-1} at Sedgwick Reserve, mostly between October and March. Mean annual temperature was 16.8 °C. Soils were loams and were classified as typic argixerolls. The production ($F = 1.958$, $P = 0.112$) and disappearance ($F = 1.333$, $P = 0.268$) of hyphae did not vary strongly or significantly over this time (B). Hyphae were produced consistently from May onward, including the particularly dry period in October. Even so, the standing abundance of hyphae varied significantly as the dry season progressed, with highest counts in April 20 (C; $F = 3.384$, $P = 0.015$). For statistical analyses, we performed repeated measures analyses of variance on ranked data, with production rate, disappearance rate, or standing hyphae as dependent variables and sampling date as the independent variable. The unit of replication was the minirhizotron tube ($n = 16$). We used hyphal counts instead of hyphal length, as our questions addressed presence/absence of fungi rather than biomass.

We found that hyphae were produced—albeit at low rates of 0.5–1.5 hyphae cm^{-2} —throughout the dry season, even when soil moisture dropped below 5% volume (Fig. 2). A number of mechanisms could have allowed fungi to remain viable even when soils were very dry (Schimel et al., 2007). For example, osmolytes (e.g., glycerol, erythritol, and mannitol) allow fungi to reduce internal water potential and deter dehydration (Witteveen and Visser, 1995). Thus, at least a portion of the fungal community was active, even though plants can be strongly affected in grasslands in this region (Xu and Baldocchi, 2004).

In addition, hyphae remained in the soil for a relatively long time. Specifically, half the hyphae were visible for at least 145 days (Fig. 3). We could not distinguish among active, dormant, or dead fungi for most of the standing hyphae, since these states were not visually distinctive in the minirhizotron images. It is possible that many of these hyphae were dead. Even so, they did not detectably decompose over this time. Slow turnover rates in our site could result from dry conditions, leading to slower metabolism rates of fungi and other decomposers (Schimel et al., 2007), lower activity rates of extracellular enzymes that would otherwise break down

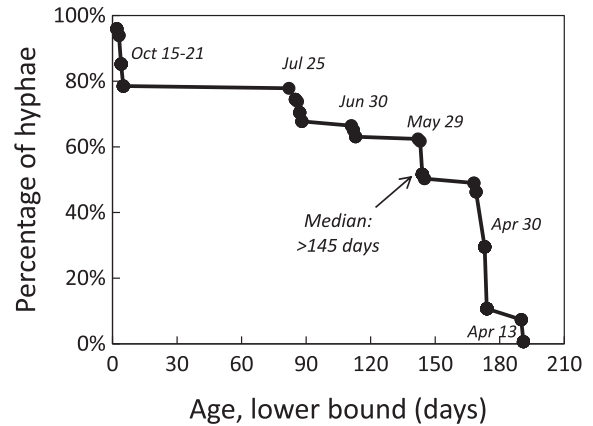


Fig. 3. Lower bounds of residence times of individual hyphae in 2008. For example, 50% of hyphae were visible for at least 145 days; 79% were visible for at least 5 days. The upper bound (191 days) was determined by the extent of the sampling period. One percent of hyphae were present throughout the entire period. A lower-bound estimate of the residence time of each hypha was determined by calculating the time period between the first (noted on figure) and last (October 15–21) sampling dates in which the hypha was visible. In every case, we could at best pinpoint the date of production or the date of disappearance, but not both. To determine exact residence times, both dates would be required. Instead, we could ascertain that a given hypha had resided in the soil for at least a certain amount of time (e.g., four days), and possibly longer. We constrained our estimates of residence times to hyphae that were present on at least one day during the high-resolution sampling period in October.

dead tissue, smaller predator populations (Gorres et al., 1999; Holmstrup et al., 2001; McSorley, 2003), and reduction of C supply to the AM members of the community (Miller et al., 1995).

These observations extend by several months the range of measured residence times of single hyphae. Measurements of dynamics of single hyphae in soils are rare, with previously-observed mean residence times of four to fourteen days (Atkinson and Watson, 2000; Bago et al., 1998; de Vries et al., 2009; Friese and Allen, 1991; Staddon et al., 2003a). Most of the preceding studies were conducted in the laboratory or greenhouse, but a field study in Michigan recorded short residence times of seven days or less (Atkinson and Watson, 2000). However, the Michigan study was conducted in early June, during the plant growing season for this ecosystem (Atkinson and Watson, 2000).

Altogether, we found little evidence that fungal dynamics were sensitive to increasing aridity in this ecosystem. Disappearance rates, production rates, and standing stocks of soil hyphae did not vary greatly as the dry season progressed (Fig. 2). The sole exception was a significantly greater hyphal standing stock early in the season, when relatively moist conditions may have been more amenable to hyphal activity. In most studies that have included dry seasons, standing hyphal lengths in the soil have declined with drought (Miller et al., 1995; Staddon et al., 2003b), with exceptions in a western Montana grassland (Lutgen et al., 2003) and a Chihuahuan desert grassland (Bell et al., 2009). In contrast, in a dry savanna, pools of microbial C, N, and P are highest in the dry season (Singh et al., 1989). Likewise, in coastal sage scrub and chaparral in Southern California, microbial N can be highest in the dry summer season (Vourlitis et al., 2009). In a global synthesis of published data, Wardle (1998) found that microbial biomass did not vary strongly among seasons in grasslands with mild climates. Microbes, including fungi in Sedgwick, may be relatively resilient to drought conditions.

In this grassland, fungal hyphae may have contributed to soil nutrient storage during the non-growing season. Nitrogen, P, and C could have been immobilized within fungal biomass for several months before being released via tissue turnover. In addition, hyphae appeared to form a relatively stable microbial network in

the soil, a portion of which was active as indicated by the production of new hyphae. The presence of active fungi during the dry season is consistent with others' observations that microbial processes can respond very quickly to moisture pulses (Xu and Baldocchi, 2004). In addition, seasonal variation in ecosystem respiration is relatively low in Mediterranean systems compared to other biomes (Falge et al., 2002). A long-lived, comparatively stable population of fungal hyphae during the dry season may be one mechanism underlying this pattern.

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