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Ecological stoichiometry of aquatic fungi: current knowledge and perspectives

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ABSTRACT

Ecological stoichiometry investigates how the ratios of elements in organisms shape their ecology and nutrient and energy fluxes in ecosystems. Despite their global distribution and essential roles in nutrient cycling, microbial decomposers are among the least known organisms in terms of elemental concentrations and stoichiometric relationships. This review compiles information currently available on aquatic fungi and the role of stoichiometric constraints in fungal ecology. These data show that elemental ratios of fungal biomass vary widely, with ranges exceeding those found for bacteria. In part, this variability may be related to hyphal growth rates, according to the growth rate hypothesis, but results have been equivocal so far and could be partly attributed to limited fungal homeostasis. However, this issue requires further investigation before firm conclusions can be drawn. Much evidence indicates that aquatic fungi enhance the quality of leaf litter to consumers by lowering C:N or C:P ratios, thereby affecting the life history of consumers and promoting nutrient and energy transfer in aquatic ecosystems. In contrast, pertinent data to assess the importance of resource stoichiometry on aquatic fungal community structure appears to be lacking at present. Differences in the stoichiometric requirements of fungi vs bacteria could partly explain literature observations on stoichiometric determinants of fungal–bacterial interaction in aquatic ecosystems. Numerous perspectives for future research unfold when applying stoichiometric theory to aquatic fungi and their role in aquatic food webs and ecosystems.

Introduction

Ecological stoichiometry (ES) is a unifying conceptual framework that focuses on how proportions of elements affect organisms and ecosystems (Sterner and Elser, 2002). A central tenet of ES is that elemental imbalances between resources and the requirements of organisms determine properties and drive ecological processes at all levels of biological

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organization, ranging from ecophysiology to population and community dynamics to ecosystem processes (Elser et al., 2000a; Sterner and Elser, 2002). Most attention has been given to the causes and consequences of variations in the carbon (C), nitrogen (N) and phosphorus (P) ratios of organisms and their resources, but the significance of other elemental ratios can also be explored effectively within the ES framework (e.g., Karimi and Folt, 2006).

Applications of ES to ecological questions are growing rapidly, but large disparities in knowledge continue to exist among taxa, ecosystem types and specific research topics. Much of ES initially focused on plankton in lakes and oceans (Redfield, 1958; Sterner and Elser, 2002) with particular attention devoted to producer–herbivore interactions (Sterner, 1990; Hessen, 1992; Elser and Hassett, 1994). However, since a large fraction of primary production is never consumed by herbivores (Cebrian, 1999), all ecosystems rely at least to some extent on dead organic matter as a major energy, carbon and nutrient source (Moore et al., 2004). This suggests that stoichiometric relationships can provide important insights into ecological and evolutionary patterns and processes involving decomposers. Stoichiometric principles have indeed been incorporated into analyses of detritivores, microbial decomposers and decomposition dynamics in both terrestrial and aquatic ecosystems (Moore et al., 2004; Martinson et al., 2008; Hall et al., 2011; Danger et al., 2013a; Mooshammer et al., 2014). However, microbial decomposers and decomposition are still among the least known organisms and processes in terms of elemental content and stoichiometric relationships. This includes fungi decomposing plant remains in streams and other freshwater environments (Danger and Chauvet, 2013).

Table 1 – Variation of measured or estimated microbial C:N:P ratios and degree of homeostasis expressed as 1/H (i.e. the slope of the log transformed relationship between elemental content of resources and consumers) in aquatic and terrestrial environments. According to Persson et al. (2010), microbes are classified as homeostatic if $0 < 1/H < 0.25$, weakly homeostatic if $0.25 < 1/H < 0.5$, weakly plastic if $0.5 < 1/H < 0.75$), and plastic if $1/H > 0.75$. na: data not available

Ecosystem	Organisms or community	Range of molar elemental ratios			Degree of homeostasis (1/H)			Growth substrate	Reference
		C:N	C:P	N:P	C:N	C:P	N:P	C source	
Aquatic	Whole microbial communities	na	na	4–92	na	na	0.34	Cellulose filter	Güsewell and Gessner, 2009 [a]
		5.9–13.4	na	na	na	na	na	Leaf litter	Pastor et al., 2014
	Bacterial communities	7–27	31–464	7–27	na	0.91	0.71	Glucose, asparagine	Tezuka, 1990
		4.7–5.7	55–176	11–31	na	0.24	0.15	Glucose	Makino and Cotner, 2004
		5.6–18.4	58–448	11–37	na	na	0.61	Glucose	Danger et al., 2008
	Bacterial cultures	3.8–11.3	77–216	10–27	na	0.19	0.08	Glucose, asparagine	Chrzanowski and Kyle 1996
		3.6–3.8	41–73	11–18	na	0.02–0.19	0–0.08	Glucose	Makino et al., 2003
		5.5–8.5	36–178	6.4–25	na	0.34	na	Glucose	Danger et al., 2008
		na	71–548	na	na	0.04–0.71	na	Glucose	Scott et al., 2012 [c]
	Fungal cultures	16.3–30.6	88–1500	3.6–53	na	0.61–0.75	0.55–0.71	Glucose	Danger and Chauvet, 2013 [c]
		12.4–17	178–218	11–16	na	na	na	Malt extract	Grimmett et al., 2013 [c]
		7.1–15.3	na	na	0.14	na	na	Glucose, methanol	Egli and Quayle 1986 (yeasts)
		7–16	40–203	5–20	0.02–0.16	0.26–0.33	0.09–0.16	Carboxymethylcellulose	Leach, 2010
Terrestrial[b]	Whole microbial communities	8.2–13.1	81–175	7.3–13.1	na	0.36	0.26	Leaf litter	Fanin et al., 2013
		6.3–9.4	32–131	4.1–36	na	na	na	Soil organic matter	Xu et al., 2013
		8.2–8.6	47–74	4.9–8.9	na	na	na	Soil organic matter	Cleveland and Liptzin, 2007
		4.9–29.3	na	na	0.14	na	na	Soil organic matter, leaf litter	Mooshammer et al., 2014
		6.4–34.1	59–860	na	na	na	na	Soil organic matter, leaf litter, wood	Manzoni et al., 2010
	Bacterial cultures	2.4–10.9	40.1–175	8.0–38	na	na	na	Lysogeny broth	Mouginot et al., 2014 [c]
	Fungal cultures	5.7–466	na	na	0.69	na	na	Glucose, asparagine	Levi and Cowling, 1969
		4.5–28.2	41.6–316	1.9–37	na	na	na	Malt and yeast extract agar	Mouginot et al., 2014 [c]
		9.6–11.9	na	na	na	na	na	Starch, urea	Ooijkaas et al., 2000

a Values based on estimates derived from data on N and P immobilization.
b Not exhaustive for soils, partly based on data from meta-analyses.
c Numbers represent minimal and maximal values among all species tested.