Current Research in Environmental & Applied Mycology (Journal of Fungal Biology)
8(4): 446–454 (2018) ISSN 2229-2225

www.creamjournal.org **Article**

Doi 10.5943/cream/8/4/4

Windows of opportunity: fruiting phenology and size of mushrooms

Halbwachs H

Bavarian Forest National Park, Danziger Str. 20, D-63916 Amorbach, Germany

Halbwachs H 2018 – Windows of opportunity: fruiting phenology and size of mushrooms. Current Research in Environmental & Applied Mycology (Journal of Fungal Biology) 8(4), 446–454, Doi 10.5943/cream/8/4/4

Abstract

The phenology of Agaricomycete fruiting is largely genetically determined, but modulated by climate and annual weather patterns. Thus, dispersal, and finally reproduction, are species-specifically optimised. Mean fruit body mass is another species-specific trait. Mean fruiting time should affect mycelial size in the sense that the mycelium of late fruiters had more time to grow than the one of early fruiters. Mycelial size is assumed to be correlated with fruit body size. I, therefore, suspected that late fruiters would have larger fruit bodies. For clarification, I extracted phenology and fruit body data from Funga Nordica and other Fungas and subjected them to statistical analyses (linear models, t-tests and ANOVA). In addition, I explored the potential relationship between ectomycorrhizal exploration types and mean fruit body size. The results show a general, significant trend for late fruiters to have larger fruit bodies. Exploration types are correlated with fruit body size, though not connected to phenology. In future studies, the probably intricate causal factors for the correlations found need to be disentangled.

Key words – Agaricomycetes – fruiting – fruit body biomass – ectomycorrhizal – saprobic – exploration types

Introduction

In recent years, the impact of climate change on macrofungal fruiting in European countries has become evident (Gange et al. 2007, Kauserud et al. 2008, 2012, Boddy et al. 2014, Andrew et al. 2018). In most cases, saprotrophic and ectomycorrhizal fruit later than several decades ago, whereby the fruiting window for the latter is still more compressed (Kauserud et al. 2012). These shifts in fruiting phenology and enhanced fungal production are likely to bear some effect on the global carbon cycle (Büntgen et al. 2013). To better appreciate such processes, a deeper understanding of the fruiting behaviour is needed.

Although climate change modulates fungal phenology, the fruiting window of mushrooms is probably largely genetically based (Selosse et al. 2001). It can be assumed that mycelial biomass grows larger with time, thus accumulating nutrients necessary for fruit body production (Moore 1998). This implies that total fruit body biomass could be affected by phenology patterns. In other words, the later a species fructifies, the more nutrients should be available to form large fruit bodies. There could also be another twist: In the case of ectomycorrhizal basidiomycetes, differential exploration types are observed (Agerer 2001) correlated with mycelial extension/coverage (Weigt et al. 2012). The larger an exploration type, the more effective becomes

Submitted 22 May 2018, Accepted 31 May 2018, Published 18 July 2018
Corresponding Author: Hans Halbwachs – e-mail – halb.wax@onlinehome.de

nitrogen foraging (Hobbie & Agerer 2010) coupled with a higher level of cellulose-degrading enzymes (Hupperts et al. 2017).

In this study, I tested the putative correlation between phenology and fruit body size by considering stipitate Agaricomycetes with lignicolous, terricolous and ectomycorrhizal lifestyles. In addition, I investigated the role of ectomycorrhizal exploration types and their biomass, which may also correlate with fruit body size.

Materials & Methods

Mean fruitbody diameter and phenological data of >2600 Agaricomycetes were extracted from the Funga Nordica (Knudsen & Vesterholt 2012). The squared fruit body diameter I used as a proxy for biomass (Tóth & Feest 2007). Species names are based on MycoBank (Anonymous 2018) and Index Fungorum (Kirk et al. 2015). For the analysis of species related to exploration types, additional fruit body size data from various sources were used (Favre 1960, Breitenbach & Kränzlin 1981–2005, Moser 1983, Alessio 1985, Papetti et al. 2000, Galli 2006, Sarnari 2007, Kuo & Contributors 2014, Landry & Contributors 2018). For the identification of exploration types I used the online data bank DEEMY (Agerer & Rambold 2005-2011).

To model a possible correlation between mean fungal phenology and fruit body size, a dataset extracted from the Funga Nordica (Knudsen & Vesterholt 2012) was used. The phenological data were separated into trophic guilds and exemplary taxa (Table 1).

Table 1 Fungal groups and taxa, sample sizes and trophic mode

Fungal group/taxon	Sample size	Trophic mode
Terricolous	753	Saprobic
Lignicolous	446	
Coprophilous	63	
Psathyrella	78	
Conocybe	51	
Mycena	84	
Entoloma	219	
Ectomycorrhizal	1026	Biotrophic
Lactarius	92	
Russula	140	
Tricholoma	57	
Inocybe	142	
Cortinarius	382	

To account for outliers, I winsorized the upper and lower 5% with the Excel add-in “RealStat 5.4” (Zaiontz 2018). The log-normalised data were fitted to linear models (“Ordinary Least Square Regression”), and calculated the coefficient of determination together with significance levels p (permutation test with 9,999 replicates) using “PAST 3.20” (Hammer et al. 2001).

The same statistical method was applied to elucidate the relationship between exploration type and fruit body biomass. Species corresponding to the exploration types I took from Agerer & Rambold (2005–2011) and matched them with phenology and fruit body size data. The relative mycelial biomass differences among the four exploration types (contact, short distance, medium distance, long distance) were estimated by visually extracting mycelial coverage data from Weigt et al. (2012).

Differences in phenology were analysed by applying an ANOVA.

Results

Almost all guilds and taxa showed differential mean phenologies (Tables 2a, b, Fig. 1).

Table 2a Phenology ANOVA p-values of the guilds and taxa listed in Table 1, part 1. Bold figures denote significant values.

	Terricol.	**Lignicol.**	**Coprophil.**	**ECM**	***Cortinarius***	***Russula***	***Lactarius***
Terricolous		1	**1,73E-05**	1	**1,52E-18**	**1,12E-06**	0,3865
Lignicolous	1		**0,0004753**	1	**2,90E-16**	**0,001467**	1
Coprophilous	**1,73E-05**	**0,0004753**		**1,31E-07**	**6,67E-16**	1	**0,004991**
Ectomycorrhizal	1	1	**1,31E-07**		**3,20E-30**	**1,94E-09**	0,1002
Cortinarius	**1,52E-18**	**2,90E-16**	**6,67E-16**	**3,20E-30**		**9,74E-33**	**1,44E-22**
Russula	**1,12E-06**	**0,001467**	1	**1,94E-09**	**9,74E-33**		0,1889
Lactarius	0,3865	1	**0,004991**	0,1002	**1,44E-22**	0,1889	
Tricholoma	1	1	**0,01035**	1	**2,29E-11**	0,6269	1
Inocybe	**8,96E-07**	**0,00566**	**0,02886**	**2,83E-10**	**3,00E-39**	1	0,08949
Entoloma	**0,02669**	1	**0,003086**	**0,004927**	**5,12E-33**	0,05216	1
Psathyrella	**5,61E-07**	**4,14E-05**	1	**2,81E-09**	**1,10E-20**	1	**0,004824**
Mycena	**5,98E-06**	**1,27E-05**	**4,59E-09**	**5,07E-08**	1	**1,94E-13**	**2,24E-09**
Conocybe	**0,00085**	**0,01928**	1	**3,67E-05**	**6,66E-16**	1	0,1363

Table 2b Phenology ANOVA p-values of the guilds and taxa listed in Table 1, part 2. Bold figures denote significant values.

	Tricholoma	***Inocybe***	***Entoloma***	***Psathyrella***	***Mycena***	***Conocybe***
Terricolous	1	**8,96E-07**	**0,02669**	**5,61E-07**	**5,98E-06**	**0,0008485**
Lignicolous	1	**0,00566**	1	**4,14E-05**	**1,27E-05**	**0,01928**
Coprophilous	**0,01035**	**0,02886**	**0,003086**	1	**4,59E-09**	1
Ectomycorrhizal	1	**2,83E-10**	**0,004927**	**2,81E-09**	**5,07E-08**	**3,67E-05**
Cortinarius	**2,29E-11**	**3,00E-39**	**5,12E-33**	**1,10E-20**	1	**6,66E-16**
Russula	0,6269	1	0,05216	1	**1,94E-13**	1
Lactarius	1	0,08949	1	**0,004824**	**2,24E-09**	0,1363
Tricholoma		0,2475	1	**0,01516**	**1,42E-05**	0,2381
Inocybe	0,2475		**0,03189**	0,07217	**9,52E-16**	1
Entoloma	1	**0,03189**		**0,001501**	**2,25E-11**	0,1122
Psathyrella	**0,01516**	0,07217	**0,001501**		**1,08E-10**	1
Mycena	**1,42E-05**	**9,52E-16**	**2,25E-11**	**1,08E-10**		**1,85E-08**
Conocybe	0,2381	1	0,1122	1	**1,85E-08**	

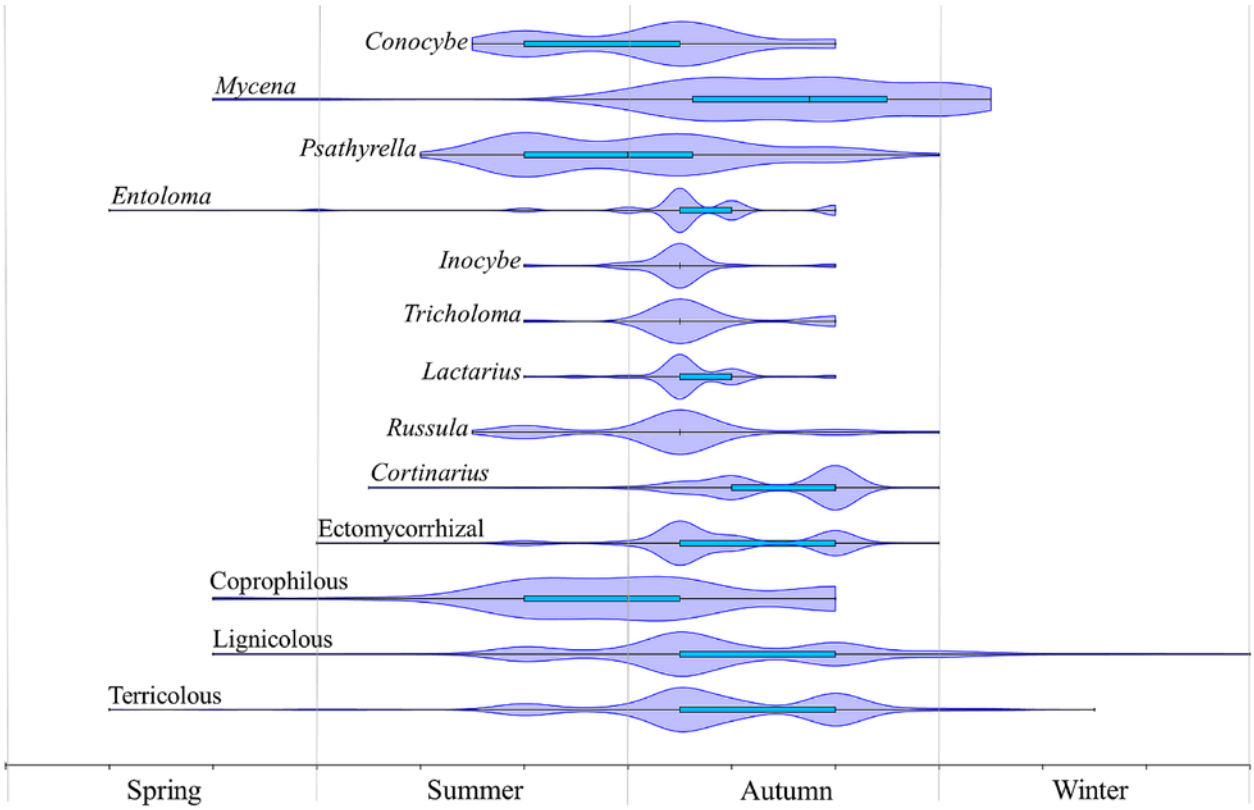

Fig. 1 – Phenology chart of the guilds and taxa listed in Table 1. Whiskers indicate standard errors. The violin-shaped envelopes show probability densities.

The regressions between mean phenology and mean fruit biomass showed heterogenous results (Table 3).

Table 3 Coefficient of correlation (r) and determination (r^2), and significance (p) of mean phenology and mean fruit body biomass regressions of the guilds and taxa listed in Table 1. Values are rounded, significance of regressions of guilds and taxa denoted with * ≤0.5. ** ≤0.01, *** ≤0.001.

	r	**r^2**	**p**
Terricolous* **	0.19	0.037	0.0001
Lignicolous	-0.038	0.0014	0.4
Coprophilous	0.07	0.005	0.6
Ectomycorrhizal* **	0.19	0.036	0.0001
Cortinarius*	0.34	0.12	0.0001
Russula*	0.17	0.03	0.05
Lactarius*	0.26	0.07	0.013
Tricholoma	0.08	0.006	0.57
Inocybe*	0.18	0.03	0.03
Entoloma*	-0.25	0.06	0.0001
Psathyrella	0.004	1.7E-05	0.97
Mycena	-0.15	0.023	0.17
Conocybe	0.17	0.03	0.23

The most significant correlation was found for *Cortinarius* (Fig. 2).

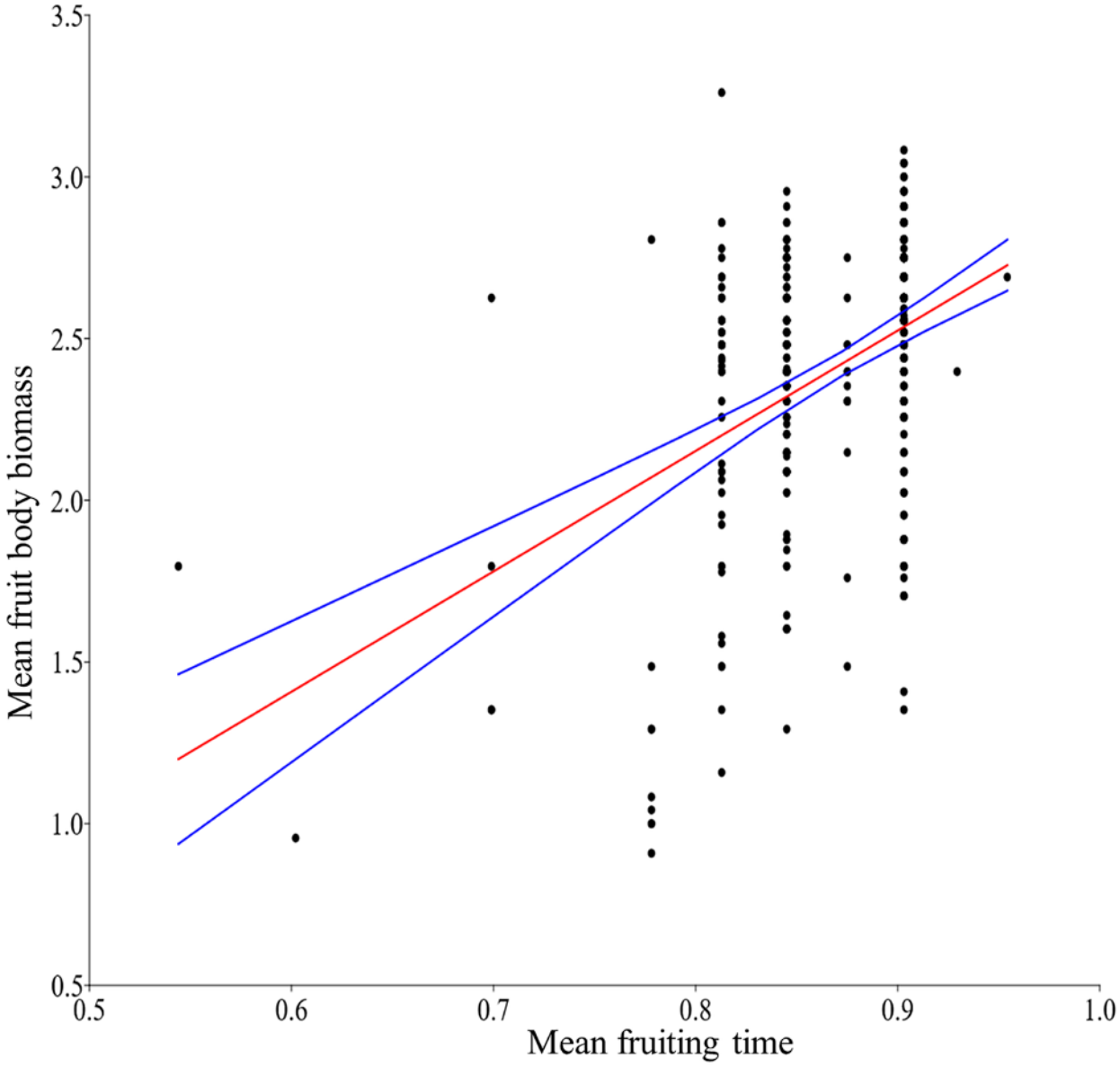

Fig. 2 – Linear regression between mean phenology and fruit body size of *Cortinarius* (r^2 0.12, p 0.0001). The blue upper and lower lines denote 95% confidence limits.

The relative mycelial coverage (proxy for biomass) of the four ectomycorrhizal exploration types were different (Table 4)

Table 4 Exploration types and their corresponding relative mycelial biomasses

Exploration type	**Rel. biomass**
Contact	0
Short distance	1
Medium distance	1.9
Long distance	3

Mean fruit body biomass of the four exploration types of the species included in this study partly differed (Fig. 3).

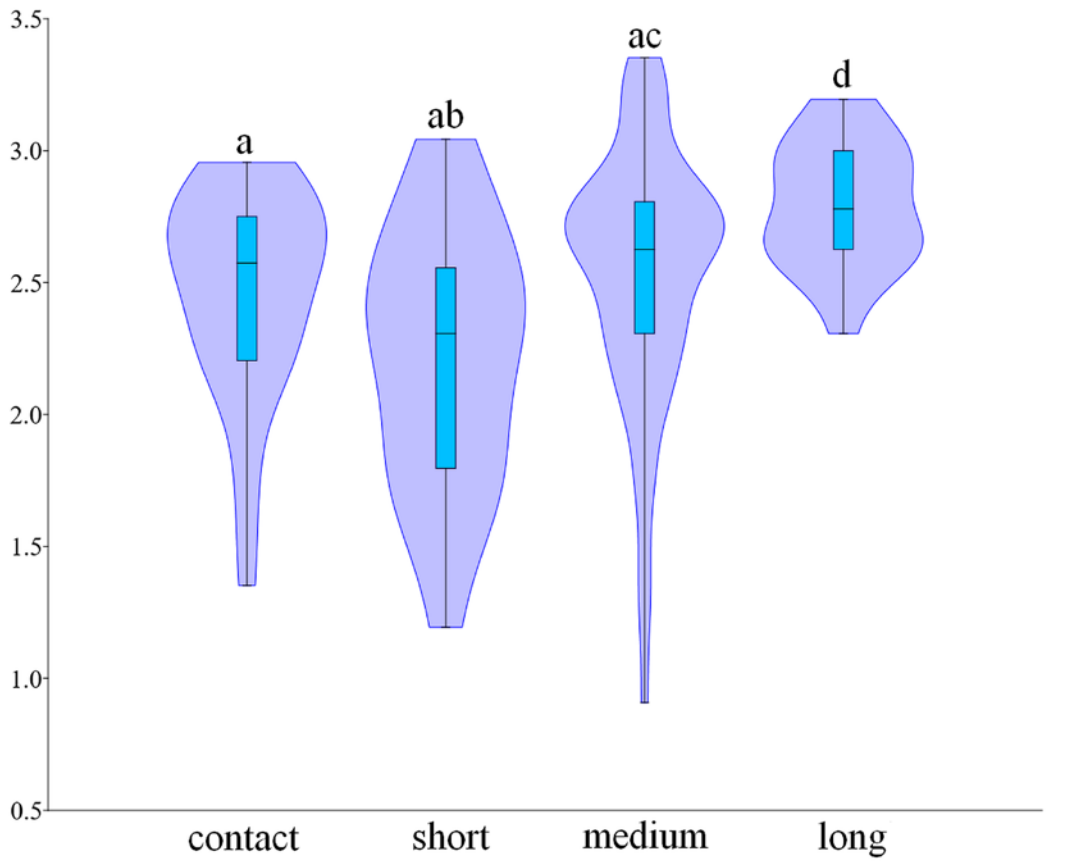

Fig. 3 – Mean fruit body biomass of the four contact types (log-normalised). Whiskers indicate standard errors. Significance differences are denoted by small letters. The violin-shaped envelopes show probability densities.

The mean phenology of the species in this dataset is not related to exploration types (ANOVA Mann-Whitney: $p > 0.5$ in all cases).

Discussion

Phenological patterns of the fungal guilds and species investigated are largely and obviously dominated by the same seasonal patterns (Fig. 1). Most terricolous and ectomycorrhizal Agaricomycetes fruit in Scandinavia during autumn. Only the coprophilous guild, *Psathyrella* and, to a lesser extent, *Conocybe* have their fruiting window overlapping summer and autumn. I suspect that in both cases the substrate (dung, manure, compost) permits an extended fruiting period, being more independent of weather patterns than e.g. terricolous fungi. The rather compressed fruiting patterns of the ectomycorrhizal fungi (Fig. 1) most probably reflect the phenology of the hosts: in autumn, carbohydrates accumulate in the roots, thus providing maximum carbon supply to the fungi (Dickie et al. 2010).

Although the signals are mostly weak (low r^2, see Table 3), the general trend appears to support the hypothesis that species typically fruiting during later seasons produce larger mean fruit body biomass, supposedly because the optimal mean mycelial size requires a minimum time to develop. *Entoloma* is a marked exception because mean fruit body size becomes smaller later in the year. The reason may be that this genus includes many early fruiters (Noordeloos 1992). It may indicate an overwintering mycelium which has grown to optimal size during the preceding year. Thus, such species potentially evade predators (Boddy & Jones 2008) and competition from other fungi. The latter suggestion is plausible because of the low number of Agaricomycetes fruiting

from early spring to summer (5.5% of 1026 ectomycorrhizal and 13.6% of 1262 saprobic species in Scandinavia).

In ectomycorrhizal Agaricomycetes, mycelial size is co-determined by their exploration types. *Cortinarius*, a medium exploration type taxon, is predominantly late fruiting with comparatively large fruit bodies. This seems to be less caused by the exploration type than by phenology because exploration type and phenology do not correlate. For instance, *Inocybe*, though belonging the short distance type, shows the same pattern as *Cortinarius*, i.e. larger fruit bodies in late fruiting species.

In conclusion, I suggest that late fruiting Agaricomycetes have larger fruit bodies than early fruiters. One may assume now that the number of fruit bodies a species typically produces would have some relevance in fruiting patterns. While there are indications that fruit body number is negatively correlated with biomass (Bässler et al. 2016), a correlation between phenology and number of fruit bodies has not been found ($p > 0.1$).

In my view, the mostly weak correlations are the result of several factors. Apart from mycelial growth as such, the following aspects may have led to species-specific phenological characteristics of Agaricomycetes coupled with belowground processes:

- Species-specific genet size
- Angio- vs gymnosperm hosts (the latter have an extended photosynthetic season: Bond (1989), but also see Bourdeau (1959))
- Competition among fungi
- Lifestyle (r-, C-, S-selected) (Andrews 1992, Andrews 2017)
- Saprobic competence of ectomycorrhizal species (Hupperts et al. 2017)
- Interaction between saprobic and ectomycorrhizal fungi (Verbruggen et al. 2017)
- Phenology of grazers such as *Collembola* (Ek et al. 1994, A'Bear et al. 2012)
- Microbial threats along annual temperature and moisture gradients
- Niche size and space (Selosse et al. 2018)
- Substrate succession (litter decomposition/quality through seasons: Couteaux et al. (1995))
- Many vascular plants can store nutrients in subterranean bulbs, rhizoms, thickened roots etc. during winter, and use these nutrients to start growing earlier and/or more vigorously. Similar storage modes are be present in macromycetes, for instance sclerotia or bulbils and storage hyphae (Clémençon et al. 2012).

There might be an additional catch with ectomycorrhizal Agaricomycetes: What if the host size affects the biomass of fruit bodies? Is, for example, the mean fruit body size of *Dryas*-associated species smaller than of *Pinus*-associated ones?

All these aspects deserve further attention in future studies.

Acknowledgements

I thank Claus Bässler (Bavarian Forest National Park) for providing a dataset containing fruit body sizes and corresponding numbers, and for inspiring discussions. Josef Simmel (University of Regensburg) provided valuable suggestions for improving the manuscript.

This work was privately financed.

References

A'Bear AD, Boddy L, Hefin Jones T. 2012 – Impacts of elevated temperature on the growth and functioning of decomposer fungi are influenced by grazing collembola. Global Change Biology 18(6), 1823–1832.

Agerer R. 2001 – Exploration types of ectomycorrhizae. Mycorrhiza 11(2), 107–114.

Agerer R, Rambold G. 2005–2011 – DEEMY – An Information System for Characterization and Determination of Ectomycorrhizae. From www.deemy.de (accessed 2018).
Alessio CL. 1985 – *Boletus* Dill. *ex* L. (Fungi Europaei 2). Giovanna Biella, Saronno.
Andrew C, Heegaard E, Gange AC, Senn-Irlet B et al. 2018 – Congruency in fungal phenology patterns across dataset sources and scales. Fungal Ecology 32, 9–17.
Andrews JH. 1992 – Fungal life-history strategies. In: Carrol GC, Wicklow DT. The fungal community: its organization and role in the ecosystem. – Marcel Dekker Inc., New York, 119–145.
Andrews JH. 2017 – Comparative Ecology of Microorganisms and Macroorganisms. Springer New York.
Anonymous. 2018 – MycoBank. International Mycological Association. http://www.mycobank.org/. (accessed 2018).
Bässler C, Halbwachs H, Karasch P, Holzer H et al. 2016 – Mean reproductive traits of fungal assemblages are correlated with resource availability. Ecology and Evolution 6(2), 582–592.
Boddy L, Büntgen U, Egli S, Gange AC et al. 2014 – Climate variation effects on fungal fruiting. Fungal Ecology 10, 20–33.
Boddy L, Jones TH. 2008 – Interactions between basidiomycota and invertebrates. In: Boddy L, Frankland JC, van West P. Ecology of saprotrophic basidiomycetes. – Elsevier, 155–179.
Bond W. 1989 – The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biological Journal of the Linnean Society 36(3), 227–249.
Bourdeau PF. 1959 – Seasonal variations of the photosynthetic efficiency of evergreen conifers. Ecology 40(1), 63–67.
Breitenbach J, Kränzlin F. 1981–2005 – Fungi of Switzerland (Vol. 1–6). Mykologia, Luzern.
Büntgen U, Peter M, Kauserud H, Egli S. 2013 – Unraveling environmental drivers of a recent increase in Swiss fungi fruiting. Global Change Biology 19(9), 2785–2794.
Clémençon H, Emmett V, Emmett EE. 2012 – Cytology and Plectology of the Hymenomycetes. J. Cramer.
Couteaux MM, Bottner P, Berg B. 1995 – Litter decomposition, climate and litter quality. Trends in ecology & evolution 10(2), 63–66.
Dickie IA, Kałucka I, Stasińska M, Oleksyn J. 2010 – Plant host drives fungal phenology. Fungal Ecology 3(4), 311–315.
Ek H, Sjögren M, Arnebrant K, Söderström B. 1994 – Extramatrical mycelial growth, biomass allocation and nitrogen uptake in ectomycorrhizal systems in response to collembolan grazing. Applied Soil Ecology 1(2), 155–169.
Favre J. 1960 – Catalogue descriptif des champignons supérieurs de la zone subalpine du Parc National suisse. Lüdin, Liestal.
Galli R. 2006 – I Lattari. Dalla Natura, Milano.
Gange AC, Gange EG, Sparks H, Boddy L. 2007 – Rapid and Recent Changes in Fungal Fruiting Patterns. Science 316, 71.
Hammer Ø, Harper DAT, Ryan PD. 2001 – PAST: Paleontological statistics software package for education and data analysis (folk.uio.no/ohammer/past). Palaeontologia Electronica 4(1), 9–11.
Hobbie EA, Agerer R. 2010 – Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. Plant and Soil 327(1–2), 71–83.
Hupperts SF, Karst J, Pritsch K, Landhäusser SM. 2017 – Host phenology and potential saprotrophism of ectomycorrhizal fungi in the boreal forest. Functional Ecology 31(1), 116–126.
Kauserud H, Heegaard E, Büntgen U, Halvorsen R et al. 2012 – Warming-induced shift in European mushroom fruiting phenology. Proceedings of the National Academy of Sciences 109(36), 14488–14493.
Kauserud H, Stige LC, Vik JO, Økland RH et al. 2008 – Mushroom fruiting and climate change. Proceedings of the National Academy of Sciences of the USA 105, 3811–3814.

Kirk P, Bridge P, Contributors. 2015 – Index Fungorum. 2018,
From http://www.indexfungorum.org (accessed 2018).
Knudsen H, Vesterholt J. 2012 – Funga Nordica: Agaricoid, boletoid, clavaroid, cyphelloid and gastroid genera. Nordsvamp, Copenhagen.
Kuo M, Contributors. 2014 – MushroomExpert.
From www.mushroomexpert.com/contributors.html (accessed 2018).
Landry J, Contributors. 2018 – Mycoquebec. From www.mycoquebec.org (accessed 2018).
Moore D. 1998 – Fungal Morphogenesis. Cambridge University Press.
Moser M. 1983 – Die Röhrlinge und Blätterpilze. Gustav Fischer, Stuttgart.
Noordeloos M. 1992 – *Entoloma* s.l. (Fungi Europaei 5). Giovanna Biella, Saronno, Italy.
Papetti C, Consiglio G, Simonini G. 2000 – Atlante fotografico dei Funghi d'Italia Vol. 1+2. Associazione Micologica Bresadola, Trento.
Sarnari M. 2007 – Monografia illustrata del Genere *Russula* in Europa, Vol. 1+2. Associazione Micologica Bresadola, Vicenca.
Selosse MA, Martin F, Le Tacon F. 2001 – Intraspecific variation in fruiting phenology in an ectomycorrhizal *Laccaria* population under Douglas fir. Mycological Research 105(05), 524–531.
Selosse MA, Schneider-Maunoury L, Martos F. 2018 – Time to re-think fungal ecology? Fungal ecological niches are often prejudged. New Phytologist 217(3), 968–972.
Tóth B, Feest A. 2007 – A simple method to assess macrofungal sporocarp biomass for investigating ecological change. Botany 85(7), 652–658.
Verbruggen E, Pena R, Fernandez CW, Soong JL. 2017 – Mycorrhizal interactions with saprotrophs and impact on soil carbon storage. Mycorrhizal Mediation of Soil. – Elsevier, 441–460.
Weigt RB, Raidl S, Verma R, Agerer R. 2012 – Exploration type-specific standard values of extramatrical mycelium–a step towards quantifying ectomycorrhizal space occupation and biomass in natural soil. Mycological Progress 11(1), 287–297.
Zaiontz C. 2018 – Real Statistics Using Excel. From www.real-statistics.com (accessed 2018).