FUNGAL BIOLOGY 115 (2011) 569–597

British Mycological Society promoting fungal science

journal homepage: www.elsevier.com/locate/funbio

Review

Population genetics of ectomycorrhizal fungi: from current knowledge to emerging directions

Greg W. DOUHAN[a,**,1], *Lucie VINCENOT*[b,***,1], *Hervé GRYTA*[c,d], *Marc-André SELOSSE*[b,*]

[a]*Department of Plant Pathology and Microbiology, University of California, Riverside, CA 92521, USA*
[b]*Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, Equipe Interactions Biotiques, 1919 Route de Mende, F-34293 Montpellier cedex 5, France*
[c]*Université de Toulouse, UPS, UMR 5174 EDB (Laboratoire Evolution et Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France*
[d]*CNRS, UMR 5174 EDB (Laboratoire Evolution et Diversité Biologique), F-31062 Toulouse, France*

ARTICLE INFO

Article history:
Received 15 November 2010
Received in revised form
6 March 2011
Accepted 12 March 2011
Available online 21 March 2011
Corresponding Editor:
Nicholas P. Money

Keywords:
Biogeography
Cryptic biological species
Ecological strategies
Fungal reproduction
Gene flow
Isolation by distance
Mating systems
Molecular markers
Population genetics
Somatic incompatibility

ABSTRACT

Ectomycorrhizal (EM) fungi are major microbial components of boreal, temperate and Mediterranean forests, as well as some tropical forest ecosystems. Nearly two decades of studies have clarified many aspects of their population biology, based on several model species from diverse lineages of fungi where the EM symbiosis evolved, *i.e.* among Hymenomycetes and, to a lesser extent, among Ascomycetes. In this review, we show how tools for individual recognition have changed, shifting from the use of somatic incompatibility reactions to dominant and non-specific markers (such as random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP)) and, more recently, to co-dominant and specific markers (such as microsatellites and single nucleotide polymorphisms (SNPs)). At the same time, the theoretical focus has also changed. In earlier studies, a major aim was the description of genet size and popul/ation strategy. For example, we show how some studies supported or challenged the simple, classical model of colonization of new forest stands by ruderal (R) species, propagating by spores and forming small genets, progressively replaced in older forests by more competitive (C) species, propagating by mycelial growth and forming larger genets. By contrast, more recent studies give insights into some genetic traits, such as partners' assortment (allo- *versus* autogamy), genetic structure of populations and gene flow that turn out to depend both on distance and on whether spores are animal- or wind-dispersed. We discuss the rising awareness that (i) many morphospecies contain cryptic biological species (often sympatric) and (ii) trans- and inter-continental species may often contain several biological species isolated by distance. Finally, we show the emergence of biogeographic approaches and call for some aspects to be developed, such as fine-scale and long-term population monitoring, analyses of

---

[*] *Corresponding author*. Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, Equipe Interactions Biotiques, 1919 Route de Mende, F-34293 Montpellier cedex 5, France.

[**] *Corresponding author*. Department of Plant Pathology and Microbiology, University of California, Riverside, CA 92521, USA. Fax: +1 951 827 4132.

[***] *Corresponding author*. Present address: IASMA-Fondazione Edmund Mach, Research and Innovation Center, via E. Mach 1, 38010 San Michele all'Adige, Italy. Tel.: +39 0461615507; Fax: +39 0461650872.

E-mail addresses: gdouhan@ucr.edu, lucie.vincenot@cefe.cnrs.fr, ma.selosse@wanadoo.fr

[1] G.W. Douhan & L. Vincenot equally contributed to this article and should be considered as associated first authors.

doi:10.1016/j.funbio.2011.03.005

subterranean populations of extra-radical mycelia, or more model species from the tropics, as well as from the Ascomycetes (whose genetic idiosyncrasies are discussed). With the rise of the '-omics' sciences, analysis of population structure for non-neutral genes is expected to develop, and forest management and conservation biology will probably profit from published and expected work.

Introduction

The mycorrhizal interaction between fungi and plant roots is a common, worldwide symbiotic interaction (Smith & Read 2008; Tedersoo *et al.* 2010) that contributed to land colonization by terrestrial plants and to their posterior diversification (Selosse & Le Tacon 1998). Although a limited fraction of the land flora associates with ectomycorrhizal (EM) fungi, EM associations are dominant among the major forest trees in the Mediterranean, temperate, boreal and some tropical regions, from the families *Pinaceae*, *Fagaceae*, *Nothofagaceae*, *Myrtaceae* and *Dipterocarpaceae*, making EM fungi ecologically relevant (Smith & Read 2008). EM association involves an estimated 6000 (Brundrett 2002) to >20 000 fungal species (Rinaldi *et al.* 2008), and is thought to have evolved at least ten times (Hibbett & Matheny 2009; Tedersoo *et al.* 2010) within the Asco- and Hymenomycetes (a subclade of Basidiomycetes). EM fungi have widely been recognised based on morphological characters, because some of them produce conspicuous epigeous fruitbodies (*Amanita*, *Boletus*, *Pisolithus*, *Russula*, *Suillus*...), but some are less obvious, producing hypogeous ('truffle-like' fungi: *Rhizopogon*, *Tuber*...) or resupinate (*Hydnellum*, *Thelephora*...) fruitbodies or even no known fruitbodies, such as the widespread *Cenococcum geophilum*. Beside their major ecological roles in some forests, EM associations are also economically important because they improve tree growth (Le Tacon *et al.* 1992; Selosse *et al.* 1998) or are sources of edible mushrooms: *ca.* 200 EM species are edible, such as truffles in Europe and matsutake mushrooms in Asia, which are both estimated to be worth over US$ 2 billion/y (Yun & Hall 2004).

Although a number of reviews have focused on various aspects of EM community ecology (Dahlberg 2001; Horton & Bruns 2001; Taylor 2002), to our knowledge no review in the last 15 y has specifically been devoted to EM population genetics (Dahlberg & Stenlid 1995; except for one review in French, Selosse 2001a), although Xu (2006) reviewed elements for molecular genetic analyses of fungal populations. Even though scarce, in terms of frequency as compared with other organisms, publications on EM population genetics are accumulating linearly at a constant rate (Figs 1 and 2), signalling a permanent interest in the EM research community. Many studies have focused on some model EM taxa, such as *Laccaria* spp., *Hebeloma cylindrosporum*, *Tricholoma matsutake*, *Suillus* spp., *Rhizopogon* spp., *C. geophilum*, and *Tuber* ssp., but beside these 'model species' investigations have also been accumulating for many other EM species from diverse ecosystems (Tables 1 and S1). Here, we review how population genetics studies have enhanced our knowledge about establishment, maintenance and dynamics of EM populations, as well as about the functioning of the EM symbiosis and biology of EM fungi under natural conditions.

The complexity of EM communities

Compared with single-partner symbiotic systems, EM symbiosis in nature acts more like a network connecting a host plant with several fungal species and individuals, and *vice versa* (Selosse *et al.* 2006). Estimations of dozens of EM species sharing the root system of the same host plant are commonly reported (Dahlberg 2001; Horton & Bruns 2001; Richard *et al.* 2004; Hynes *et al.* 2010). As a result, many fungal and host species co-exist in a forest stand. Moreover, greenhouse and *in vitro* experiments have also found large quantitative variation even among isolates of the same species for traits involved in mycorrhizal functioning, *e.g.* the capacity to form EM associations or to use soil nutrients (*e.g.* di Battista *et al.* 1996; Guidot *et al.* 2005).

First attempts to understand the diversity and ecology of communities of EM fungi were based on the distribution of epigeous fruitbodies and the below-ground distribution of colonised mycorrhizal root tips, as characterised by gross morphology (*e.g.* Agerer 1991, 1995). However, the observed root tip morphotypes often correlated poorly with described epigeous fungal fruitbodies (*e.g.* Nylund *et al.* 1995). More recently, molecular tools such as restriction fragment length polymorphisms (RFLPs) and/or sequencing of the internal transcribed spacer (ITS) of the ribosomal DNA from individual root tips (Gardes & Bruns 1996; Begerow *et al.* 2010) greatly enhanced the identification of EM species directly on host roots. In a review on EM community ecology, Horton & Bruns (2001) emphasised three general features: (i) there is generally a poor correspondence, in terms of species identity and abundance, between fungi found as above-ground fruitbodies and fungi identified on EM roots (Gardes & Bruns 1996; Peay *et al.* 2007); (ii) underground EM communities show high diversity and species often have patchy distribution (*e.g.* Richard *et al.* 2004, 2005); and (iii) at least some abundant EM species can be shared by different hosts (including some understory herbs, see Selosse *et al.* 2004).

Studies of EM populations: evolution of tools...

Historically, a first step in the ecological study of EM fungi applied the concepts and methods of population genetics (see Glossary) to EM fungi, in order to characterise the genetic diversity and distribution of specific species. Early studies used somatic incompatibility (SI) reactions that had been previously used for many saprotrophic and pathogenic fungi: hyphal fusion between different mycelia is stable only between genetically similar individuals, while genetically dissimilar ones produce a reaction zone (Worrall 1997; Glass & Fleissner 2006).