

Intraclonal genetic variation: ecological and evolutionary aspects.

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Arbuscular mycorrhizal fungi: genetics of multigenomic, clonal networks and its ecological consequences

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Arbuscular mycorrhizal fungi are thought to have remained asexual for 400 million years, although recent studies have suggested that considerable genetic and phenotypic variation could potentially exist in populations. A brief discussion of these multigenomic organisms is presented. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **79**, 59–60.

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Arbuscular mycorrhizal fungi (AMF) are zygomycete fungi that form symbioses with over 60% of plant species. These fungi have been known for many years to improve plant phosphorus nutrition and plant growth (Smith & Read, 1997). More recently, the diversity of these fungi at the species level has been shown to positively affect the diversity and functioning of plant communities (van der Heijden *et al.*, 1998; van der Heijden, 2002) and therefore they play an important role in the functioning of ecosystems. These fungi are thought to have remained asexual for 400 million years, although recent studies on both AMF genetics and heredity of traits suggests that considerable genetic (Sanders *et al.*, 1995; Sanders, Clapp & Wiemken, 1996) and phenotypic variation (Bever & Morton, 1999) could potentially exist in AMF populations. Such studies of variation in these supposedly clonal populations are valuable because they can help to determine at what level AMF diversity is ecologically important. However, they also have a practical value in commercial inocula development. Studies of genetic and phenotypic variation can help to identify how many different phenotypes are likely to be present in a population and how many different AMF should be isolated from that population and put into

an inoculum to represent the functional and genetic diversity that might occur naturally in the field.

AMF certainly display unusual levels of within-individual genetic diversity. AMF form coenocytic hyphal networks that act below-ground as connections among plants of different species. Our group has recently demonstrated that this genetic diversity is partly due to the fact that the many nuclei contained within each individual have genetically diverged from each other to form a population of multiple genomes (Kuhn, Hijri & Sanders, 2001). Some evidence exists that this is due to the absence of recombination among AMF and the lack of genetic bottlenecks in the life cycle that limit the amount of genetic material that is inherited in future generations (Sanders, 2002a). The detection of recombination in an organism in which genetically different nuclei coexist poses many problems, and in particular presents serious difficulties for applying population genetic models such as calculations of index of association. One way around this problem is to use phylogenetic-based methods for detecting recombination, as demonstrated by Kuhn *et al.* (2001).

Given that mycorrhizal fungi are multigenomic, are ecologically important and that a population of an AMF could form a clonal network in which movement of genetic material could cause considerable genetic heterogeneity, it is surprising that there are, to date, no

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studies on the biology and genetics of a population of these fungi. Obviously, few models in ecology or evolutionary biology take into account that more than one genome could be inherited by offspring in each generation and therefore many of the current theories and models are difficult to apply to understanding the evolution of these fungi. It is easily imaginable that in a multigenomic hyphal network considerable genetic and phenotypic differences could occur, either by selection on nuclear genotypes in different parts of the network or by a type of drift where different nuclei are segregated by chance during the formation of new spores (Sanders, 2002a; Sanders, 2002b). Therefore, we have taken a population biological approach to studying the ecology of these multigenomic organisms to see if there is a genetic basis for any observed phenotypic variation in an AMF population. Studying a population of these fungi requires obtaining isolates of a number of individuals from a field site and then cultivating them over several generations in identical environmental conditions to remove maternal effects. Preliminary studies on a population of *Glomus intraradices* Schenck & Smith that was isolated from a field site and cultivated in such a way have shown that phenotypic and genetic variation in a population of AMF is very high at a local scale within a 90 × 90 m field (A. Koch & G. Kuhn, unpubl. data). Variation in the fungal phenotype, with respect to hyphal density, was high, indicating that such differences in the phenotype could potentially affect the efficacy of the symbiosis.

Clearly, variation in these clonal, multigenomic organisms is interesting to study in both an evolutionary and ecological perspective since models of evolution have not previously been applied to a multigenomic organism. We advocate the study of AMF population biology in order to understand how mechanisms such as selection and drift act on the genomes of these fungi to create the unexpectedly

high genetic and phenotypic variation that we have seen in these organisms.

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