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SANNI FÄRKKILÄ

Methods for studying plant-fungal interactions – reflecting on the old, the new and the upcoming

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UNIVERSITY OF TARTU
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1632

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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in Botany and Mycology at the University of Tartu on December 11th, 2023 by the Scientific Council of the Institute of Ecology and Earth Sciences University of Tartu.

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Commencement:	Oecologicum (J. Liivi 2, Tartu), room 127, on 9th of February 2024 at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu

ISSN 1024-6479 (print)
ISBN 978-9916-27-444-6 (print)
ISSN 2806-2140 (pdf)
ISBN 978-9916-27-445-3 (pdf)

University of Tartu Press
www.tyk.ee

CONTENTS

LIST OF ABBREVIATIONS

AM	Arbuscular mycorrhizal
CLSM	Confocal laser scanning microscopy
CMN	Common mycorrhizal network
CQD	Carbon quantum dot
DLS	Dynamic light scattering
EM	Ectomycorrhizal
FNP	Fluorescent nanoparticle
FTIR	Fourier transform infrared microscopy
ITS	Internal transcribed spacer
LOD	Limit of detection
MBC	Minimum biocidal concentration
NMDS	Non-metric multidimensional scaling
OTU	Operational taxonomic unit
PL	Photoluminescence
STEM	Scanning transmission electron microscopy
TEM	Transmission electron microscopy
QD	Quantum dot
XPS	X-ray photoelectron spectroscopy
YPD	Yeast-peptone-dextrose

LIST OF PUBLICATIONS

The thesis is based on the following publications, denoted by bold roman numerals.

I. Färkkilä, S. M. A., Kiers, E. T., Jaaniso, R., Mäeorg, U., Leblanc, R. M., Treseder, K. K., Kang, Z., Tedersoo, L., 2021. Fluorescent nanoparticles as tools in ecology and physiology. Biological Reviews 96, 2392–2424. https://doi.org/10.1111/BRV.12758

II. Färkkilä S. M. A., Valtonen A., Saravesi K., Anslan S., Markkola A., Kontunen-Soppela S., 2023. The effects of geographic origin and genotype on fungal diversity of silver birch (*Betula pendula*), Fungal Ecology 63, 101241. https://doi.org/10.1016/j.funeco.2023.101241

III. Färkkilä S. M. A., Mortimer M., Jaaniso R., Kahru A., Kiisk V., Kikas A., Kozlova J., Kurvet I., Mäeorg U., Otsus M., Kasemets K., 2023. Comparison of toxicity and cellular uptake of CdSe/ZnS and carbon quantum dots for molecular tracking using *Saccharomyces cerevisiae* as a fungal model. Nanomaterials 2024, 14, 10.

Author's contribution to each publication

I. I was the main conceiver of the idea for the publication, performed the literature search, wrote the manuscript with input from co-authors, submitted and revised the manuscript with input from co-authors.

II. I was involved in conceiving the idea for the publication, performed the lab work with guidance from co-authors, analysed the data with guidance from co-authors, wrote the manuscript with input from co-authors, submitted and revised the manuscript with input from co-authors.

III. I was the main conceiver of the idea for the publication, performed the laboratory work related toxicity and uptake assessments with guidance from co-authors, was involved in particle characterisation and wrote, submitted and revised the manuscript with input from co-authors.

INTRODUCTION

The importance of soil organisms in global ecosystem services, as well as local level ecosystem dynamics has been increasingly recognized (Bever et al., 2010). However, studying them, and the ecosystems they inhabit, is challenging. As they are belowground, and mostly microscopic in size, many of the methods utilized aboveground are not applicable to soil ecosystems. The development of DNA metabarcoding and other molecular techniques has given rise to a massive accumulation of biodiversity information on soil organisms during the last decades (Tiedje et al., 1999). However, we should not exclusively focus on explorative studies, in which samples are collected and sequenced, and a list of taxa reported, but attempt to address ecological hypothesis and ultimately gain more knowledge about the underlying workings of the natural world. Indeed, despite the accumulation of metabarcoding data, we still know comparatively little about the biotic drivers affecting soil communities, and about the functions of individual soil organisms. The development and utilization of a suitable suit of methods is therefore instrumental for the understanding and maintenance of these ecosystems and their taxa.

Plant roots are a good starting point for soil ecosystem studies, as they are directly linked to the aboveground ecosystems (Bever et al., 2010). Roots are also a site particularly rich in interactions and organisms, as many soil animals, protists, bacteria and fungi are particularly abundant in and around the roots, in the area known as the rhizosphere (Izumi & Finlay, 2011). Plants can be considered foundational species, because genetic and phenotypic changes in their traits may affect a multitude of interacting organisms including root, rhizosphere and foliar microbes, pollinators and herbivores, and indirectly the predators (Linhart & Grant, 1996). Indeed, plant species has been shown to be a major driver of root fungal community composition (Ishida et al., 2007), and plant genotype has been shown to influence communities of foliar fungi. On the other hand, soil organisms can also have profound effects on vegetation dynamics (Y. Liu et al., 2021; Pineda et al., 2010; Wubs et al., 2016). For example, symbiotic or pathogenic fungi in and around plant roots form dynamic communities, which may significantly benefit or hinder the growth and fitness of the plant (Alberton et al., 2009; Begum et al., 2019; Cahill et al., 2008; Hartley & Gange, 2009; Tedersoo et al., 2020; Wubs et al., 2016). Furthermore, past vegetation may affect current vegetation through soil legacies (Hannula et al., 2021; Putten et al., 2013), which may aid or obstruct the growth of new plants via the microbial communities in the soil.

Among root inhabiting fungi, so-called mycorrhizal fungi are particularly important (Smith & Read, 2008; Tedersoo et al., 2020) These fungi form a symbiosis with plant roots that usually garners nutritional benefits (Smith & Read, 2008), although their mutualistic nature is nowadays not considered a given in all circumstances (Hoeksema et al., 2010). The mycorrhizal symbiosis is particularly interesting due to its global and taxonomic prevalence (Davison et al., 2015; Tedersoo et al., 2014) ancient nature (Bonfante & Genre, 2008; Tedersoo et al.,

2010), and ecological impact (Tedersoo et al., 2020). Indeed, in addition to their important role in plant nutrition, mycorrhizae can have positive effects for plant pathogen and stress resistance, as well as pollination and herbivory (M. Chen et al., 2018; Delavaux et al., 2017; Jung et al., 2012; Koricheva et al., 2009; Pozo & Azcón-Aguilar, 2007). However, the study of these fungi comes with the additional challenge that their hyphae can encompass large areas of the soil, while being extremely fragile (Henriksson et al., 2023; Karst et al., 2023). Furthermore, fungal taxonomy is under constant change due to the accumulation of DNA-based information, and species delimitation morphologically, but also genetically. Many fungi also have a complex reproductive cycle including clonal as well as sexual reproduction, and hyphae of two individuals are able to fuse together by a process called anastomosis (Smith & Read, 2008). A recent study on arbuscular mycorrhizal (AM) fungi showed that the same fungal cell may possess nuclei of two different genotypes (Kokkoris et al., 2020). Thus, the study of mycorrhizae comes with its own set of challenges, which require methods that take into account their unique features.

Another example of the unique features of fungi, is the concept of so-called common mycorrhizal networks (CMNs), and their role in plant community dynamics (Jakobsen, 2004; Leake et al., 2004; Simard et al., 2012). For most of the 20th century, it has been commonly accepted that a CMN connects roots of different plants to each other and acts as a conduit for different molecules (Barto et al., 2011; Leake et al., 2004; Oelmüller, 2019; Selosse et al., 2006; Simard et al., 2012; Van Der Heijden & Horton, 2009; Walder et al., 2012). It has been suggested that carbon (Avital et al., 2022; Cahanovitc et al., 2022; Carey et al., 2004; Deslippe & Simard, 2011; Klein et al., 2016; D. Robinson & Fitter, 1999; Simard, Durall, et al., 1997; Simard, Perry, et al., 1997; Watkins et al., 1996), nutrients (X. He et al., 2004, 2005, 2006, 2009; Y. He et al., 2019a, 2019b; Meding & Zasoski, 2008; Mikkelsen et al., 2008; Muneer et al., 2023; Ren et al., 2013; Rogers et al., 2001; Tuffen et al., 2002; Wilson et al., 2006), water (Egerton-Warburton et al., 2007; Warren et al., 2008) and chemical messages (Achatz & Rillig, 2014; Babikova et al., 2013; Barto et al., 2012; Song et al., 2010, 2013, 2014; Thomas & Cooper, 2022) can be transported from one plant to another through CMNs, enabling the plants of a given ecosystem to "communicate" and even support each other (Booth & Hoeksema, 2010; Dickie et al., 2002; McGuire, 2007; Nara & Hogetsu, 2004; van der Heijden, 2004). In recent years, this narrative has captivated the public and widely disseminated in the media as factual (Karst et al., 2023; D. G. Robinson et al., 2023). However, although these networks, their structures and functions have been under research for a relatively long time (Björkman, 1960; Newman, 1988; Reid & Woods, 1969), our knowledge on their true nature and ecological significance remains limited. Moreover, many studies have reported that such CMN resource transfer did not occur (Pfeffer et al., 2004; Voets et al., 2008; Zabinski et al., 2002), the magnitude of transfer was ecologically insignificant (Cheng & Baumgartner, 2004; Nakano-Hylander & Olsson, 2007; Teste et al., 2009) or the transferred compound remained in fungal structures only (Fitter et al., 1998; Graves et al., 1997; Wu et al.,

2001). Yet, the so-called mother tree hypothesis has generally been accepted by the scientific community and the public. However, a recent meta-analysis revealed a bias in how CMN related results are cited and warned about the spread of misinformation on CMNs (Karst et al., 2023). This opener prompted several other experts to question the narrative (Blatt et al., 2023; Henriksson et al., 2023; D. G. Robinson et al., 2023), and revived the academic discussion on CMNs.

Critiques about CMNs highlight issues in the isotope labelling methods used to obtain the results that underline this narrative and question their ability to justify drawn conclusions (Henriksson et al., 2023; Karst et al., 2023). This critique is not new, as a commentary on the shortcomings of the technique has been published already two decades ago (D. Robinson & Fitter, 1999). One of the main issues relates to the separation of transfer via CMNs from transfer via alternative pathways, such as root grafts between the donor and receiver, or release of isotope in donor root exudates, which are taken up by receiver plant mycorrhizae or roots directly or following diffusion through the soil column (X. H. He et al., 2003; Henriksson et al., 2023; Karst et al., 2023). In isotope labelling experiments, the presence and magnitude of transfer are typically studied by destructively measuring the concentration of subject isotope in the receiver plant(s) after the labelling of a donor plant (X. H. He et al., 2003). Thus, it is not possible to directly observe the transfer and the way it happens; one can only make assumptions based on excluding different possibilities (Henriksson et al., 2023; Karst et al., 2023). Further, in many cases, the measurement of label isotope is done by mass-spectrometry based approaches, which cannot differentiate isotope content in plant root tissues from that contained within fungal tissues in and around the roots (Henriksson et al., 2023). Thus, unless the isotope is found in stems and/or leaves of the receiver plants, potential interplant transfer cannot be separated from allocation between fungal structures (Fitter et al., 1998; D. Robinson & Fitter, 1999; Henriksson et al., 2023). Therefore, major improvements on the experimental set-ups of isotopic experiments or entirely novel alternative methods are needed to get a clear understanding of the transfer.

Indeed, during the 20th century, it became common to utilize different control treatments such as mesh barriers, rotating growth cores and air gaps, with the aim to account for alternative transfer pathways. The most common solution for trying to eliminate non-hyphal transfer pathways, is to establish a metal or nylon mesh between the donor and receiver plants to manipulate the pathways available (Barto et al., 2012; Cheng & Baumgartner, 2004; X. He et al., 2004; Song et al., 2010; Wilson et al., 2006). For example, a mesh with a pore size that is too small for the roots but not too small for fungal hyphae has been used to exclude root contact. Similarly, meshes with a pore size smaller than fungal hyphae have been used as a control treatment for assessing the contribution of soil diffusion only. Yet, these treatments have been considered inadequate, as roots pushing against the mesh from both sides might still enable non-mycorrhizal nutrient transfer via diffusion, and conversely a mycorrhizal connection could form in such roots even by diffusion through mesh only (Fitter et al., 1998). Furthermore, the lower rate of transfer in treatments with a non-mycorrhiza permeating mesh could be

explained by the fact that the ratio of surface area of the mesh material versus the actual pores is much more favourable when the pore size is bigger (Henrikssen et al., 2023). In response to these issues, mesocosm experiments with meshes separated by a gap (Barto et al., 2012; Fall et al., 2022; X. He et al., 2005; Meding & Zasoski, 2008), mesh bags inserted further away from each other (Deslippe & Simard, 2011; Mikkelsen et al., 2008), as well as trenching or other means of severing of the soil, hyphae or roots were implemented (Deslippe & Simard, 2011; Gyuricza et al., 2010; Voets et al., 2008). Still, it has been argued that the apparent positive effects of CMNs in these cases may be due to the increase in exploration volume available in the hyphal treatment, and/or due to negative effects of the lack of space for roots and hyphae in the control (Karst et al. 2023). Furthermore, ingrowth cores (Johnson et al., 2001; Leifheit et al., 2014) that enabled regular spinning of the core to sever hyphal connections were developed to enable a new non-mycorrhizal control treatment (Achatz & Rillig, 2014; Barto et al., 2012). In many cases, naturally non-mycorrhizal plants, mycorrhizae deficient mutants, or plants of different mycorrhizal type were established as controls. However, it has been argued, that these are not adequate control treatments, as the benefits of a particular mycorrhizal type *per se* may be larger than those of another type, even if a CMN is not formed (Henrikssen et al., 2023; Karst et al., 2023). On the other hand, genetic approaches have been used for confirmation of a hyphal connection between the donor and receiver, to indicate that the mycorrhizal transfer pathway between the two is available (Avital et al., 2022; Cahanovitc et al., 2022). However, the presence of the same taxonomic unit, or even fungal genet, in the roots of the plants does not prove that the hyphal connection is intact (Henriksson et al., 2023; Karst et al., 2023).

To ensure that the carbon or nutrients applied are actually going through the host plant, improvements have also been made to the labelling methods. For instance, several low concentration pulses of labelled CO_2 administered into bagged donor plants, while the ground around the plant is covered, may help eliminate direct or soil mediated receiver uptake of label from the air (Philip & Simard, 2008). Furthermore, a control plant placed near the donor plant can be used to account for potential leakage from the bag or release through root respiration taking place outside the labelling bag. In a few cases, the isotope content of fungal fatty acids within plants has been analysed (Nakano-Hylander & Olsson, 2007; Voets et al., 2008). As these fatty acids can only be formed in fungi, their presence in plants would entail that the carbon came from fungi. However, this method has so far not shown transfer of labelled fatty acids to plant tissues. Additionally, instead of adding labelled phosphorus or nitrogen to the donor soil, it may be given by dipping the leaves or branches of donor plants into tubes of nutrient solution, which helps to eliminate the possibility of receiver roots or hyphae taking up the nutrients directly from donor soil (X. H. He et al., 2003). However, despite how much the experimental set-ups for isotopic labelling have developed over the years, it has been argued that if this method is used, it may never be possible to reliably exclude all alternative transfer pathways (Henriksson et al., 2023; Karst et al., 2023). A novel method that is not based on isotopes is

therefore needed to concretely assess the existence and magnitude of CMN interplant resource transfer (Karst et al., 2023).

A potential solution for overcoming the issues of isotope labelling is the utilization of so-called fluorescent nanoparticles (FNPs) as labels for nutrient transfer (Karst et al., 2023; Whiteside et al., 2009). In terms of the CMN C and nutrient transfer, the biggest potential advantage of FNP tracking is that the particle movement can be observed in real time, *in vivo* (Agarwal et al., 2015; Dahan et al., 2003; S. L. Liu et al., 2016; van't Padje, Oyarte Galvez, et al., 2020) This entails the possibility to observe the nutrient movement itself, instead of simply confirming that nutrient transport of some sort has occurred (Chan & Nie, 1998). As the name implies, FNPs are particles ranging in size from a few nanometres to around 100 nm. FNPs release energy as light upon excitation with a suitable light source (Bera et al., 2010; Chan & Nie, 1998). The particles are composed of different inorganic or organic materials, and can emit light in various wavelengths depending on their composition and size (Bera et al., 2010; Resch-Genger et al., 2008). Bare FNPs can be used to track individuals or organs (Ekvall et al., 2013; Minnaar & Anderson, 2019), while particles connected to a molecule of interest, such as a nutrient compound, enable tracking its movement within organisms (Brandt et al., 2015; Erland et al., 2019; Whiteside et al., 2019) with an accuracy of up to a few nanometres (Holtzer et al., 2007; Jonas et al., 2006). However, while FNPs are intensively researched and developed for technical and medical applications, only a brave few have applied them to answer physiological or ecological questions (**I.**). In terms of fungi, the use of FNPs has so far been limited mostly to arbuscular mycorrhizal fungi, and the work has depended on a particular person, either directly (Whiteside, Digman, et al., 2012; Whiteside et al., 2009, 2019; Whiteside, Garcia, et al., 2012), or indirectly (van 't Padje et al., 2021, 2022; van't Padje, Oyarte Galvez, et al., 2020; van't Padje, Werner, et al., 2020). Thus, it is important to further assess the suitability of this method for fungal nutrient tracking, both in theory and in practice, and in relation to other fungal systems.

Despite the eminent potential of FNP nutrient tracking, this approach has its own pitfalls. One of the potential issues is that the previously mentioned AM studies, as most biological studies, utilize only a single type of FNP: a type of semiconductor quantum dot (QD), which contains the hazardous heavy metal cadmium (Cd) (**I.**). There are many studies reporting a multitude of adverse responses of Cd-containing QDs, and the general census is that their use in biological systems should be avoided (N. Chen et al., 2012; Oh et al., 2016; Pelley et al., 2009; Sharma et al., 2017; Wang & Tang, 2018; Winnik & Maysinger, 2013). Thus, the development of ways to reduce particle toxicity, and the development of new particle types altogether, is important (Filali et al., 2020; Reiss et al., 2016; Winnik & Maysinger, 2013; Xu et al., 2016). The properties of FNPs may be improved by the addition of shells or coatings (Vasudevan et al., 2015), or by doping, i.e. the incorporation of additional chemical elements into the particle (Park et al., 2016). Indeed, it has been shown that encasing the Cd-containing particle core in a shell can markedly reduce the adverse effects (Mei et al., 2014;

Vasudevan et al., 2015; Winnik & Maysinger, 2013). Yet, these particles remain difficult and unpleasant to synthesize due to the need for several complex steps including toxic precursors, and their purchase, especially in quantities needed for whole-plant experiments, is expensive (**I.**). Thus, especially long-term, eliminating the need for such hazardous metals in FNPs is a better option.

Among the recently developed cadmium-free FNP types, so-called carbon quantum dots (CQDs), often referred to simply as carbon dots, have received a lot of attention (S. N. Baker & Baker, 2010; Li et al., 2012; Lim et al., 2015). As they consist of biologically abundant elements and are simple and cost-effective to prepare, they have been dubbed as the new "it" dot that may replace semiconductor QDs in the future (Alas et al., 2020; Gayen et al., 2019; Yang et al., 2009). However, these particles also come with several challenges, including a lack of clarity on the origin of their fluorescence (Cayuela et al., 2016; Dekaliuk et al., 2014; Goryacheva et al., 2017; Zhu et al., 2015), major differences in the properties of CQDs depending on synthesis precursors and methodologies (Dekaliuk et al., 2014; Esfandiari et al., 2019; Fan et al., 2019) as well as a lack of general quality standards, application protocols and nomenclature (Cayuela et al., 2016; Dekaliuk et al., 2014; Essner et al., 2018). Thus, the application of CQDs requires more preliminary analyses and testing, as well as knowledge of chemistry and physics, than the application of commercial semiconductor QDs (**I.**). Experimental comparisons of Cd-containing QDs and CQDs are rare and focus solely on the comparison of toxicity profiles of the particles, not on other aspects of their applicability for biological studies (**I.**). Thus, it is not only unclear whether the technique is applicable to CMN research *per se*, but also unclear which, if any, particle type is suitable for the purpose.

With this knowledge gap in mind, the main aim of the thesis was to assess the theoretical (**I.**) and practical (**III.**) applicability of various FNPs for mycorrhizal nutrient tracking. The theoretical suitability of the particles was assessed by careful familiarisation into the technique and the previous studies utilizing FNPs (**I.**). However, as we attempted to execute practical experiments, we encountered several problems, and were unable to replicate previously reported results. After several futile attempts with FNPs, mycorrhizae, soil and plants, it became clear that working experiments in such a complex study system would require considerably more time and more trial and error than what could be fitted into a PhD degree. Furthermore, the replacement of isotopes for FNPs in fungal nutrient tracking also received critique (Raven, 2022). The only reasonable option was to start from the beginning and the basic assumptions that need to be met for the technique to work. One pertinent assumption is that the FNPs are able to move into and within fungal systems, preferably in similar ways as the nutrients would (Kuyper et al., 2023; Raven, 2022). To test this, we utilized the yeast *Saccharomyces cerevisiae* as a fungal model, to assess how different FNPs interact with fungal cells (**III.**). Like mycorrhizal fungi, *S. cerevisiae* possesses a rigid cell wall, which may act as major barrier for FNP uptake. However, due to its short

life cycle and the vast amount of information on its nutrient dynamics, nanoparticle interactions and imaging, it may serve as proxy for other fungal cells, without the complexity of CMNs.

As highlighted, the selection of a suitable experimental method is never simple, as each method presents its own limitations, challenges and drawbacks. Similarly, there is always a trade-off between the control and precision of lab-based experiments and the level of comparability between the experimental set-up and a natural system. Although we were forced to resort to an in vitro proof of concept study on FNPs, work on plant-fungal interactions continued in parallel, with the more established metabarcoding method (**II**). The utilization of this method allowed for an experiment in near-natural conditions, in a common garden (de Villemereuil et al., 2015), where we explored the effect plant genotype has on the community composition of root-inhabiting fungi. In addition, information gathered from the unpublished preliminary experiments on FNPs is included and discussed, as it adds to the practical knowledge on the utilization of FNPs. Moving from a theoretical methodological synthesis (**I.**) to a traditional ecological experiment (**II.**) and zooming into the molecular level (**III.**) this thesis transects the study of plant fungal interactions with a varied set of methods. Thus, it offers not only results from a metabarcoding study and a proof of concept FNP study of fungi, but also a chance to reflect on old, established and novel methods, their development and use and on the best ways of studying plant-fungal interactions now and in the future.

Aims and hypothesis

Each paper had a specific aim, in particular:

1. Assess the usefulness of fluorescent nanoparticles for biological research based on previous studies and comparisons to other methods (**I**.)
2. Study whether birch trees originating from different localities or different individuals of a population would have differences in the fungal interactions in their roots (**II**.)
3. Test whether cadmium-containing quantum dotsand carbon quantum dots are able to enter yeast cells without causing adverse effects, and whether one type of quantum dot shows more potential for common mycorrhizal nutrient tracking than the other (**III**.).

Additionally, the following hypothesis were tested:

1. Trees originating from different localities harbour different root fungal communities as predicted by the ecological mosaic theory (**II.**)
2. Individual tree genotypes have differences in their fungal communities due to the formation of community phenotypes (**II.**)

3. Fungi take up fluorescent nanoparticles only when conjugated to a nutrient source, as fluorescent nanoparticles on their own are not useful to them (**III.**)
4. Fluorescent nanoparticles with a carbon core are more biocompatible than the quantum dots containing cadmium (**III.**).

MATERIALS AND METHODS

Literature review

Literature was mined using a combination of systematic (database search with relevant keywords) and inductive (extraction of referenced and citing articles from relevant papers) approaches. For paper **III.,** a single search of papers from ISI Web of Science was performed, using the keywords "quantum dot" OR "carbon dot" AND yeast* OR Saccharomyces OR Candida. For paper **I.** several searches from multiple databases (Web of Science, EBSCO and SciFinder) were performed to ensure best possible coverage of the search. In terms of sensing applications of FNPs, if multiple papers focused on the sensing of the same ion or molecule, the paper reporting the lowest limit of detection (LOD) was included in the review. Relevant medical applications were included in the introduction, but not thoroughly reviewed and not included in the main body. Relevant toxicological papers were included in a separate section. Papers from journals with an impact factor of <1 were excluded, as well as papers from reportedly predatory journals (**I.**, **III**).

Experimental set-up and sampling for metabarcoding

For paper **II.**, four trees of Silver birch (*Betula pendula*) were sampled from each of four different localities (Kittilä (67°N), Rovaniemi (66°N), Vehmersalmi (62°N) and Loppi (60°N)) and micropropagated. Four clones of all sampled trees (N_t=64) were planted in a common garden field in Joensuu, Finland, in a randomized block design (Fig. 1). The common garden field was established as a part of a larger project aimed at studying the acclimation of Silver birch to climate change, and contained additional birch clones that were not considered in the experiment at hand.

Trees were planted 1.2 m away from each other in four blocks, each of which harboured one clone of each genotype. After five growing seasons, roots from two to three opposite sides of each tree were traced from the trunk and harvested. Sampled root clumps were stored in a –20 °C freezer until further processing. Aboveground biomass and tree height, as well as the nutrient levels of the common garden field were also recorded.

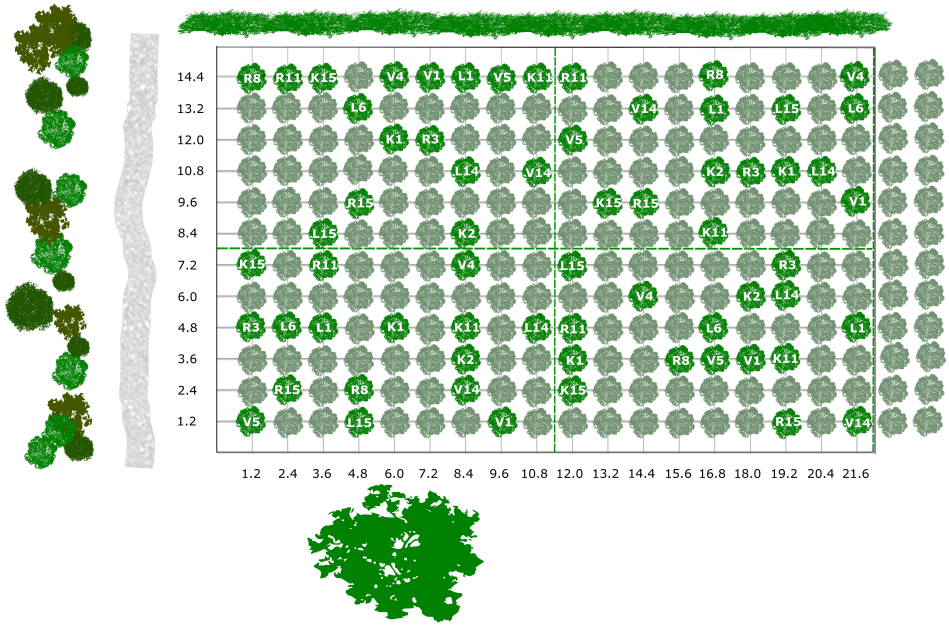

Fig. 1. A schematic representation of sampled Betula pendula trees in the common garden field in Joensuu (62°N), Finland. Numbers next to the grid signify distance in meters (m) and the borders of four blocks are marked with dashed, green lines. The genotype codes of each tree represent the four geographic origins (provenances) they originate from (Kittilä 67°N, Rovaniemi 66°N, Vehmersalmi 62°N and Loppi 60°N). Figure from Färkkilä et al. 2023.

Root sample processing, DNA extraction and sequencing

Sampled roots (**II.**) were cleaned, fine roots with a thickness of <2 mm detached, freeze dried and pulverised. DNA was extracted from the powdered samples using the Power soil DNA extraction kit, and fungal internal transcribed spacer 2 (ITS2) -regions were amplified by PCR with the fITS7 (GTGARTCATCGAATC TTTG) (Ihrmark et al., 2012) primer. A uniquely tagged ITS4 primer (CCTCCG CTTATTGATATGC) (White et al., 1990) was added for multiplexing. The PCR reaction mixture included 2 µl of template DNA (with a concentration of 5 ug/ul), 9.4 µl of nuclease-free water, 4 µl of buffer solution (5x Phusion High-Fidelty buffer, Thermo Scientific), 0.4 µl of dNTP's (10 µM), 2 µl of each primer (2 µM) and 0.2 µl DNA polymerase (Phusion High-Fidelty DNA Polymerase, 2 U/µl, Thermo Scientific). The reaction volume was 20 µl and samples were amplified in duplicate, which were later pooled for sequencing. A negative control with nuclease free water was included in each microplate. PCR conditions included 1 min at 98 °C followed by 27 cycles with a 10 s denaturation period at 98 °C, a 20 s annealing period at 57 °C, a 30 s elongation period at 72 °C and a final elongation period of 7 mins at 72 °C after all cycles were complete. PCR samples were

kept at 4 °C prior following analyses. The success of the PCR reaction was confirmed by gel-electrophoresis, and the concentration and quality of the DNA measured. The extracted DNA was purified and sequenced with an Ion Torrent sequencer.

Bioinformatics and statistics

Sequence data (**II.**) was processed with the PipeCraft 2 bioinformatics pipeline (Anslan et al., 2017) prior to statistical analysis. Sequences were demultiplexed, quality filtered and clustered, and taxonomy was assigned based on the UNITE database (Nilsson et al., 2019). Singletons and operational taxonomic units (OTUs) of unknown taxonomy, as well as OTUs identified as non-fungal, were excluded from analysis. PERMANOVA and PERMDISP tests were performed in PRIMER-e with the PERMANOVA+ extension (Anderson et al., 2008). Tree origin was used as a fixed term, while genotype was included as a random factor nested within the origin. The experimental block of the sampled tree was added to the model as a random factor and the number of reads per sample (Tedersoo et al., 2022) as well as tree aboveground biomass and coordinate positions in the common garden field were included as covariates. Accumulation curves of OTUs per origin and genotype were produced with R's the iNEXT package (Hsieh et al., 2016). non-metric multidimensional scaling (NMDS) figures illustrating differences in OTU composition between origins and genotypes were made with the vegan package (Oksanen et al., 2020) in R.

Tested FNP types, synthesis of carbon quantum dots (CQDs) and particle conjugation

Two types of FNPs were selected for practical testing (**III.**) based on the literature review (**I.**). Commercially prepared CdSe/ZnS semiconductor quantum dots (QDs), with a carboxylic acid capping were purchased from Thermo Fisher (QDot ITK 565, Invitrogen, Carlsbad, California, USA). This particle type was selected because they were found to be the most commonly utilized FNPs in biological applications, including in the previous studies with AM fungi (**I.**). Carbon cored quantum dots (CQDs) were prepared in-house from citric acid and cysteine, following a hydrothermal microwave method (Suner et al., 2021). CQDs were selected as a non-cadmium containing alternative to test, as previous studies had shown that these are under intensive development and have good biocompatibility (**I.**). The synthesis method was selected based on the accuracy of reporting and ease of synthesis. Cysteine was selected as the amino-acid of interest, as it has been shown that AM fungi willingly take up cysteine conjugated QDs (Whiteside, Garcia, et al., 2012). Thus, the CQD synthesis protocol that was chosen also included cysteine as one of the precursors. CdSe/Zns QDs were connected to cysteine in-house, following the protocol of the manufacturer. Prior to this, we

made several attempts at conjugation according to the previously reported protocol (Whiteside et al., 2009), but the resulting particles were extremely aggregated (Fig. 2), and the XPS (X-ray photoelectron spectroscopy) analysis did not show evidence for successful conjugation. As previous reports on AM fungi indicated that fungi would not take up QDs without the amino acid (Whiteside, Digman, et al., 2012; Whiteside et al., 2009; Whiteside, Garcia, et al., 2012), unconjugated CdSe/ZnS QDs were used as a control. Thus, the experiment (**III.**) included three particle treatments: bare and conjugated QDs and CQDs.

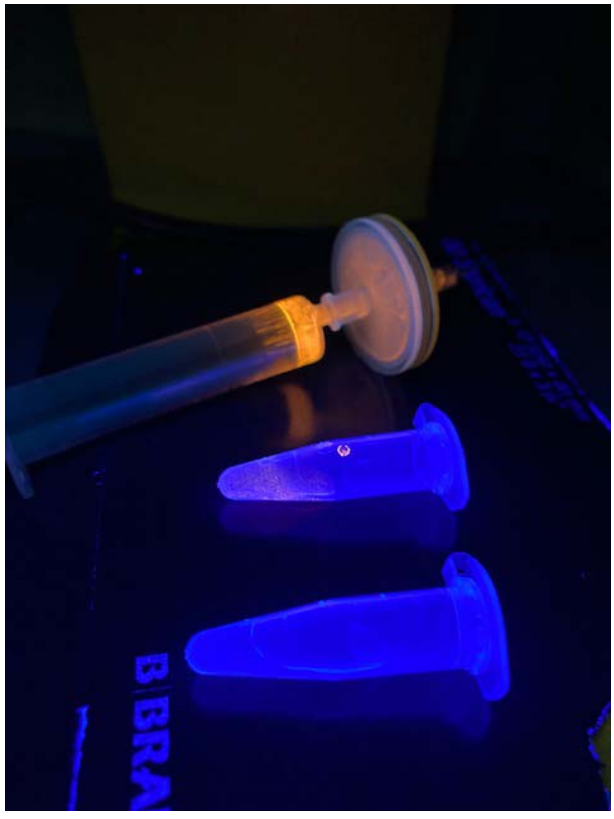

Fig. 2. Aggregated CdSe/ZnS quantum dots (QDs) under an UV lamp, after conjugation to cysteine performed according to Whiteside et al. (2009). Pristine solution in the syringe, QDs filtered through a 0.45 µm syringe filter in the middle and QDs filtered through 0.22 µm syringe filter in the front. Visual inspection of fluorescence shows that a considerable part of the particles were too large to pass the 0.45 µm filter, and very few, if any, passed the 0.22 µm filter. Thus, particles are much too large to be taken up by cells.

Characterisation of FNP properties

As highlighted by several experts (**I.**), one of the biggest issues with CQDs is that the synthesised products are not sufficiently characterized (Cayuela et al., 2016; Essner et al., 2018). Therefore, for paper **III.** self-synthesized CQDs were characterized in terms of their fluorescence properties and chemical composition, by measuring the emission and excitation spectra and quantum yield, and by characterizing the composition with XPS and FTIR (Fourier transform infrared microscopy). Successful conjugation of cysteine to CdSe/ZnS QDs was also confirmed with XPS. Primary sizes of all particles were assayed with (S)TEM ((scanning) transmission electron microscopy). The hydrodynamic sizes i.e., the sizes of particles in solution, and surface charges were assessed with dynamic light scattering (DLS).

Toxicity and uptake of FNPs

Nanoparticle toxicity, especially for the particles containing Cd, is a relevant concern when working with FNPs. Particle toxicity may vary not only by elemental composition, but by size, surface charge, shape and synthesis precursors (**I.**). Toxic effects are also usually concentration and time dependent, and differ by the organism (**I.**). Thus, for the practical experiment (**III.**), we tested the toxicity of all FNPs in conditions, concentrations and exposure times that matched those used in the uptake assay. Therefore, a spot test (Suppi et al., 2015) with *S. cerevisiae* (strain BY4741) exposed to serial dilutions of 0.1 to 100 mg/L of the different QDs was conducted. The minimum biocidal concentrations (MBC), in which the growth of yeast cells is inhibited, were assessed after 1h or 24 h exposure time. Yeast cells suspended in deionized water were pipetted into the wells of a microplate containing the particle solutions, as well as positive ($AgNO_3$) and negative (deionized water) controls. After exposure, droplets from each well were pipetted into a standard yeast-peptone-dextrose (YPD) agar culture plate and the colony formation in the spots was visually assessed after 72 h.

For uptake estimation, yeast cells were stained with a cell-membrane specific dye, washed, exposed to 1 or 100 mg/L QDs for 24 h and observed under a confocal laser scanning microscope (CLSM). Stained cells kept in plain deionized water were used to prepare control slides. Slides were prepared by either directly pipetting the exposed cells to microscopy slides and drying at 37 °C or by washing the cells prior to pipetting onto the microscopy slides for drying. This was done to assess the strength of particle interactions and to remove loosely bound or free QDs from the solution. After cell suspensions had dried on the slide, a drop of fixing solution and a cover glass were placed on top. Stacked images of cells in various areas of the samples were captured with the CLSM, and compared to images of control cells. The uptake of QDs by yeast cells was confirmed by moving to the middle of the image stacks and observing whether the QD signal was present in the cells or only at the sides and/or at the top or bottom of the image stack.

FNP interactions with soil (unpublished)

Additionally, a series of unpublished preliminary experiments were conducted. Amongst these, results related to particle interactions with soil are formally included in this thesis. Other observations made during the project are discussed in later sections when relevant. For the spot measurements from soil, different concentrations and volumes of different FNPs were added to the soil. The effect of the volume/concentration ratio, method of application, sieving and mixing on the evenness and strength of the fluorescence signal were assessed. Signal persistence in soil was studied by re-measuring the samples and comparing the measured values to previously obtained ones. The samples were excited using either 405 nm laser diode or the 3rd harmonic of pulsed Nd:YAG laser (355 nm). The illuminated area was a circular spot of ~4 mm in diameter (unfocused beam). The sample was placed on a motorised stage, which was scanned either along a line or in both directions, using step size of 5 or 10 mm. Fluorescence was recorded with Andor Shamrock (Oxford Instruments, Abingdon UK) SR303i spectrometer equipped with a cooled Andor Newton EMCCD camera. Depending on the signal strength, the collection time was 0.5–2 seconds whereas the spectral resolution was 0.5–1.5 nm. The spectra were corrected to the spectral response of the system. Where applicable, the measured signal was divided by the product of collection time and slit width, to make the photoluminescence (PL) intensities comparable across experiments.

RESULTS

In paper **I**. we presented a tabular database of FNP studies in life sciences, including ~150 relevant publications for easy referencing in later studies. Based on these data, most studies have been performed using cadmium-containing quantum dots, more specifically CdSe/ZnS QDs. For CQDs, the most common application is sensing of various ions and chemicals. Furthermore, we presented a table comparing key properties of different FNP types as well as fluorescent dyes to aid particle selection (Table 1., Färkkilä et al. 2021). We also revised the classification of particle types and presented a uniform terminology for them (Fig. 3., Färkkilä et al. 2021). The reviewed studies revealed some challenges and discrepancies related to FNPs, but none the less illustrated the potential advantages of FNPs. Information from the paper was also used in the planning of follow-up experiments, including those presented in paper **III.**

Table 1. Key properties of major fluorescent nanoparticle (FNP) types and fluorescent dyes. Values in parentheses indicate maximums when outliers are included. Table form Färkkilä et al. 2021.

Property	Traditional QD (Cd)	Carbon-based dot	Alternative FNP	Fluorescent dye
Ease of application	high	medium	low	very high
Data availability	high	medium	low	very high
Commercial availability	high	medium	low	very high
Cost	high	low	low to high	low
Difficulty of synthesis	high	low to medium	medium	low
Quantum yield (%)	30–<100	0–<95	0–80	<90
Separation of spectra	high	medium to high	medium to high	low
NIR suitability	high	medium	low to high	low to medium
Fluorescence lifetime (ns)*	10–100	<100	up to 200	1–10
Signal precision	high	high	ND	low
Stability	high	high	ND	low
Colour tunability	high	medium	medium	not possible
Multimodality	yes	yes	yes (theoretical)	no
Biocompatibility	low	medium to high	low to high	high
Toxicity	high	low to medium	low to medium	low to high
Water solubility	low to medium	medium to high	low to medium	low to high
Size (nm)	2–10(20)	<10(100)	1.4–25	~0.5
Type-specific limitation	blinking	unreliability of existing data	heterogeneity, lack of data	sensitivity to microenvironment

*Not taking into account afterglow particles
ND, not experimentally determined; NIR, near-infrared; QD, quantum dot.

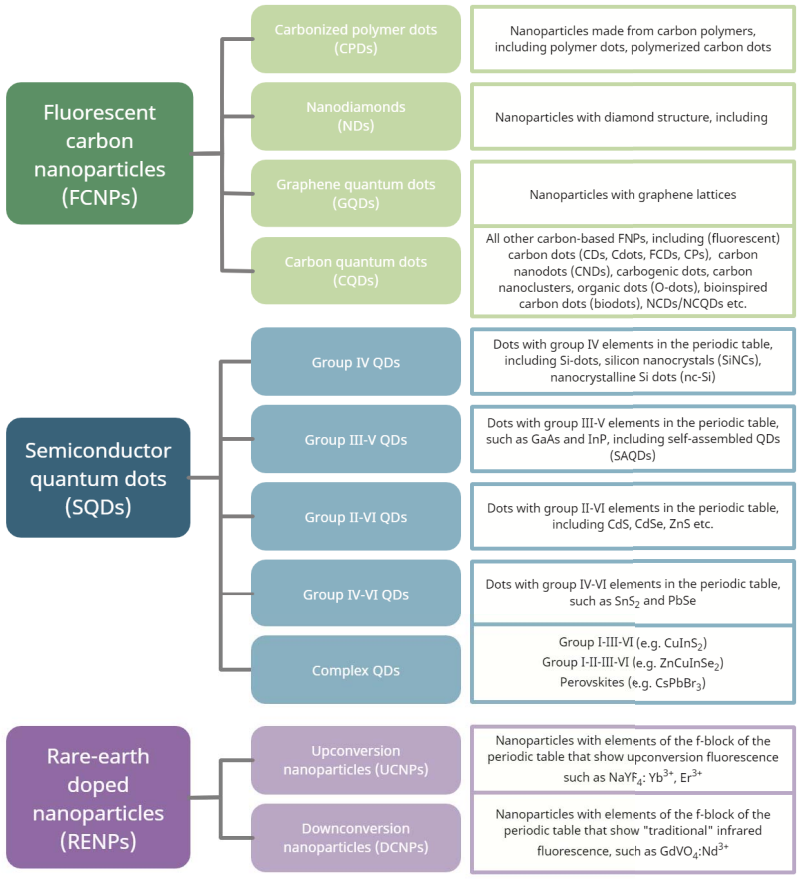

Fig. 3. Proposed classification of fluorescent nanoparticles (FNPs). The major FNP groups include fluorescent carbon nanoparticles (FCNPs), semiconductor quantum dots (SQDs) and rare-earth doped nanoparticles (RENPs). Their subgroups and information about previously used terminology are indicated. Figure from Färkkilä et al. 2021.

In paper **II**. we found that there was a significant difference in the degree of variation in root fungal communities between genotypes (PERMDISP, $F_{15, 48} = 3.30$, $p(MC) = 0.011$). Furthermore, we found that there was a significant difference between fungal OTU richness between genotypes (Fig. 4., Färkkilä et al. 2023), but not between origins. However, neither locality nor genotype had a significant effect on community composition (PERMANOVA $P > 0.5$). Tree location on the field did not explain community composition, nor did the above-ground biomass of the trees (PERMANOVA $P > 0.5$). Based on these findings, the first hypothesis (1.) that trees originating from different localities harbour different root fungal communities was rejected. Conversely, the data provided support to the second hypothesis (2. individual tree genotypes have differences in their fungal communities), as the degree of variation between fungal communities of particular genotypes differed. Furthermore, as seen in Fig. 4, there were several genotypes for which the confidence intervals (coloured backgrounds of each line) do not overlap. Although we did not correct for multiple testing, this indicates that different genotypes varied in their abilities to accumulate fungal taxa.

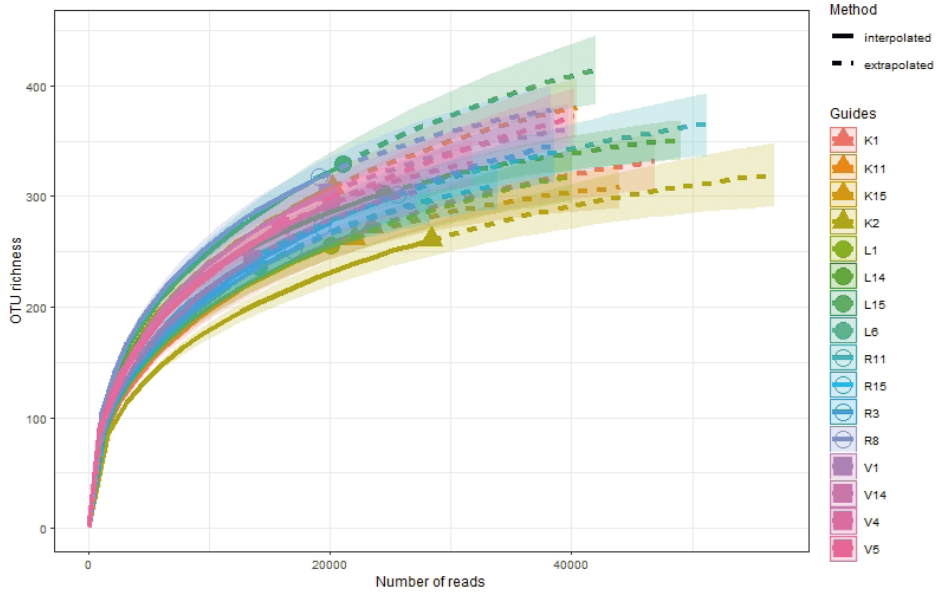

Fig. 4. Sample-size based rarefaction (solid lines) and extrapolation (dashed lines) curves of OTU (operational taxonomic units) diversity by different genotypes of Betula pendula grown in a common garden field. Genotypes originating from the same latitude share the same symbol. Coloured backgrounds of each line represent 95% confidence intervals. Figure from Färkkilä et al 2023.

In paper **III**. we showed that the self-synthesised CQDs possessed a quantum yield of ~65% and were smaller in size than commercial QDs. Furthermore, the cysteine was successfully connected to CdSe/ZnS QDs, and a corresponding set of peaks were observed in CQDs but not in pristine CdSe/ZnS QDs (Fig. 5, Färkkilä et al., 2024).

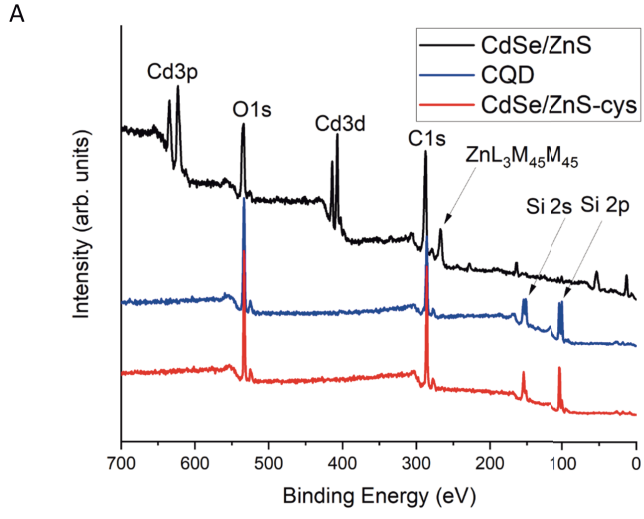

Fig. 5. The survey XPS spectra of quantum dots. The origins of the main peaks are indicated. The Si signal originates from the substrate and is particularly visible for thin samples. Figure from Färkkilä et al. 2024.

The CLSM (Fig. 6, Färkkilä et al., 2024) showed that despite being connected to a nutrient source, the semiconductor QDs were not able to enter yeast cells. They were observed to adsorb onto the surfaces of yeast cells, but washing of cells detached them. Conversely, CQD entry to cells and localisation into cell cytoplasm was observed, and the signal was preserved after washing.

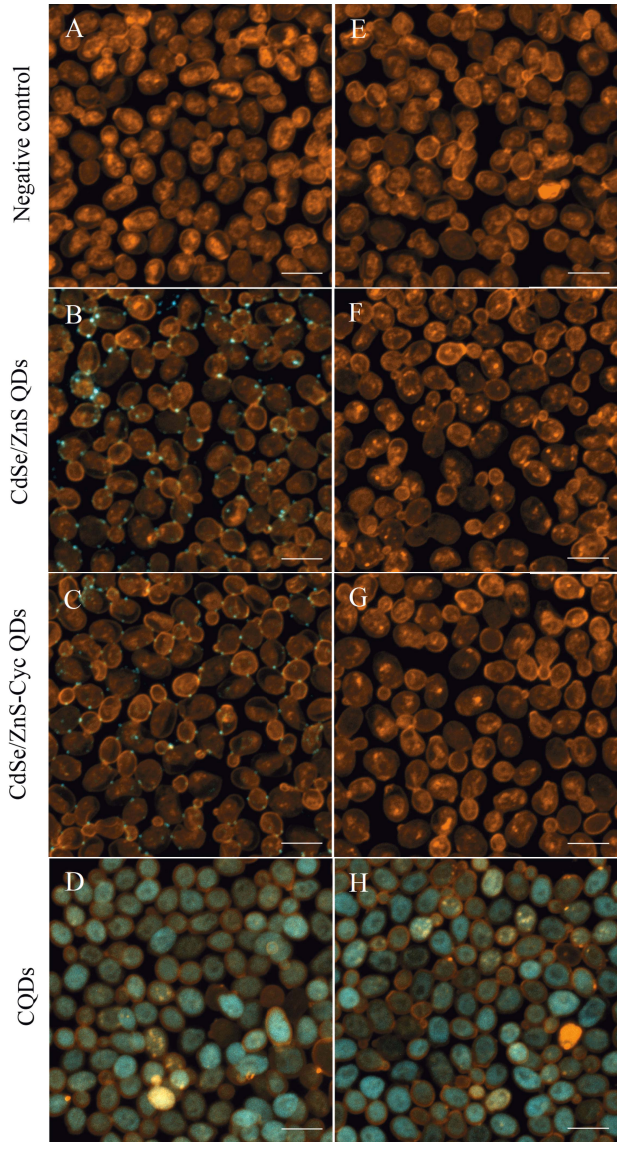

Fig. 6. Confocal laser scanning microscopy (CLSM) images of cellular interactions of quantum dots (QDs). *S. cerevisiae* BY4741 cells stained with CellBrite Fix 555 membrane stain (orange pseudocolour) were incubated with QDs (blue pseudocolour) for 24 h. After the incubation, cells were either not-washed (A-D) or washed (E-F) with MilliQ water to assess the strength of interactions. Scale bars correspond to 5 µm. Figure from Färkkilä et al., 2024.

Both particle types showed an MBC value of >100 mg/L as revealed by the spot test (Fig. 7, Färkkilä et al., 2024). All QD exposed colonies grew normally, while the negative control showed an MBC of 0.5 mg Ag/L.

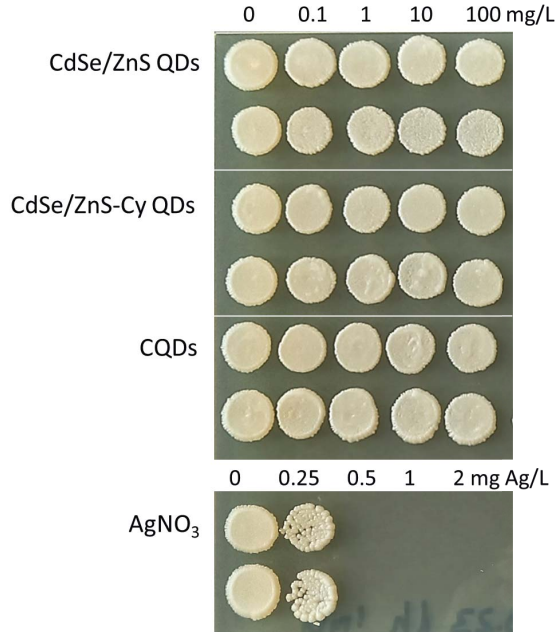

Fig. 7. A viability assay (spot test) showing the colony-forming ability of yeast *S. cerevisiae* BY4741 after 24 h of exposure to CdSe/ZnS quantum dots (QDs), CdSe/ZnS QDs connected to cysteine, and carbon quantum dots (CQDs) and $AgNO_3$ (as a positive control) in MilliQ water at 30 °C. Two replicates per tested compound were presented. Figure from Färkkilä et al., 2024.

Here, hypothesis 3. (fungi take up FNPs only when conjugated to a nutrient source) was not supported, as nutrient conjugated CdSe/ZnS QDs did not enter fungal cells. Likewise, hypothesis 4. (FNPs with a carbon core are more biocompatible than the QDs containing cadmium (Cd)) was not supported by the data, as neither the CQDs nor Cd-containing QDs negatively affected yeast growth in the tested concentrations. However, CQDs may still be more suited for fungal nutrient tracking, as unlike the Cd-containing QDs, they were able to enter the cells. These observations highlight the need to test any basic assumptions related to FNPs, and remind us of how little we know about the interactions of FNPs and fungi.

The experiments on the interactions of soil and FNPs showed that the fluorescence label distributes unevenly despite mixing and that the fluorescence signal in the soil weakens over time (Fig. 8). Although a larger solution volume and the removal of larger material by sieving make the distribution of fluorescence more even, homogeneous labelling of soil is not possible.

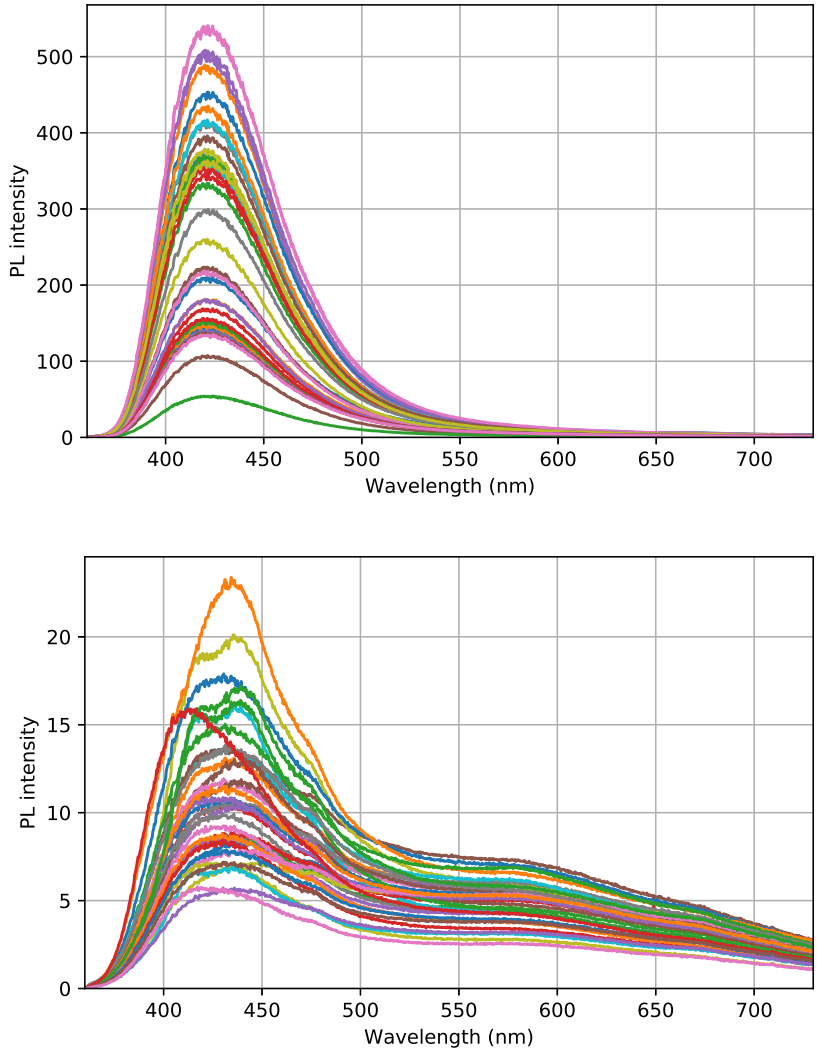

Fig. 8. Fluorescence intensity of a soil sample measured directly after label application (A) and re-measured one week later (B). Different curves represent fluorescence signals from different spots on a standard petri dish filled with live soil. The heterogeneity of the signal is evident in the large variation of signal strengths in different spots. Comparison of photoluminescence (PL) intensities in A and B shows a large decrease in signal strength between the first and second measurements.

DISCUSSION

It is no secret that the final thesis is rather different from what was originally planned. While there are experimental results with some interesting stand-alone conclusions, which are more thoroughly discussed in the respective papers, the thesis as a whole invites a discussion on the past and future of the methods to study plant-fungal interactions. It shows that novel methods may bring novel challenges, that a simple idea in theory may be more problematic in practice, and that old methods can give new and interesting results, too.

Although the development and implementation of new methods is essential for the progress of science, the problems that appeared during the execution of the FNP experiments showed that such a process may be long and frustrating. When previous data are scarce and there are no general protocols to follow, many preliminary tests are needed. In the case of the current project, we lacked basic knowledge on how the particles behave in the soil column (**I**). We did not know if, and how, FNPs would bind to the soil particles, how fast they would diffuse in the soil, or how moist the soil needed to be for the particles to be able to move. While we did manage to obtain some information about the interaction of soil and FNPs, as soil is notoriously heterogeneous and complex, and filled with different organisms and molecules that all confound experiments (Henriksson et al., 2023), it was not a reasonable place to start. Before FNP experiments in live soil can truly work, FNP and soil interactions still need further study. The challenges I faced while testing the FNP method illustrate that when attempting to implement novel tools, one should always start from the simple things and basic assumptions. In paper **III**., we showed that even in conditions in which all the confounding aspects of soil and interacting species were removed, the semiconductor quantum dots I had been trying to utilize were unable to enter fungal cells. This is no doubt one of the reasons why the more complex experiments that were tried did not yield any results. It is also a perfect example of a basic assumption that should have been tested in the beginning of the project.

The literature review (**I**.) showed FNPs as a much more promising tool than they turned out to be in practice. It is clear that FNPs can and have given answers that would be difficult to obtain with other methods. However, the vast majority of the experiments have been done with animal systems (**I.**). Out of the papers dealing with plants, many utilize tissue cultures, and very few have incorporated the soil environment (**I.**). Similarly, fungi are typically studied in pure cultures only (**I.**). Both plants and fungi, unlike animals, possess a cell wall, which may hinder particle uptake (Sun et al., 2021). The reports on uptake and interaction of FNPs in animal cells are therefore not necessarily applicable for plants and fungi. Thus, there is a significant gap between the existing FNP studies and ecologically relevant experiments with plants and fungi (**I.**). Until this gap is bridged by sequentially increasing the complexity of the experimental set-up, FNPs may be more suited to answering physiological, rather than ecological questions. Indeed, Kuyper et al. (2023) also assert that FNPs are useful for visualisation, but not suitable for mycorrhizal resource tracking at the moment. Furthermore, even the studies that have been performed in simple, controlled systems often show very

contrasting results. This is evident even in the case of *S. cerevisiae*, for which uptake and toxicity of FNPs varies between different studies (**III**.). Therefore, it is very important to avoid assumptions based on previous studies, unless the particle (down to synthesis protocol or manufacturer) and experimental system are identical. This also illustrates that, in practice, we still know very little about the interactions of fungi and FNPs. Thus, FNP tracking is far from a routine method in a fungal ecologist's tool kit. This, like any new method, should not be used just because it is new. It should only be used if it is truly better suited for answering a particular question than the previously used methods.

Our results on uptake and toxicity of FNPs to yeast (**III.**) include observations that, on the surface, go against common assumptions about the interactions between FNPs and cells. The observation that the tested CdSe/ZnS QDs were non-toxic in the spot test, shows that the presumption that all Cd-containing QDs are toxic (**I.**), does not necessarily hold in all cases. Equally surprising is the fact that these particles did not enter the cells, despite being commercially produced for this purpose. The most likely explanation for this is the particle size. It is well known that the size of nanoparticles is one of the main factors affecting their toxicity and uptake (Bilal et al., 2019; Oh et al., 2016). Smaller particle size generally aids uptake but also increases toxicity (Fan et al., 2019; Hardman, 2006). Although the primary size of the CdSe/ZnS QDs was small (around 10 nm), once removed from the buffer solution that they came in, they formed large aggregates (~300 nm). In contrast, the CQDs had a small average size (~6 nm) even in solution. Thus, the observed lack of toxicity and uptake of CdSe/ZnS QDs most likely relates to their large size, while CQD uptake is explained by their small size. Particle size is also important because a point of critique for FNP tracking in the past has been that as cell uptake of nutrient molecules and large particles like FNPs happens via different mechanisms, FNP-conjugated nutrient movement should not be used to study real nutrient movement (Kuyper et al., 2023; Raven, 2022). Thus, our results indicate that when choosing particles for molecular tracking purposes, it is important to consider not only the elemental composition of the particles but also their hydrodynamic size. On the other hand, the results show that many of the theoretically promising attributes of CQDs (**I.**) may hold also in practice. Indeed, the efficient fluorescence properties, non-toxic composition, and small hydrodynamic size of the prepared CQDs are all indicators of their potential for such tracking applications. Although more research is needed to understand the specificity of CQD uptake, these particles could provide a viable option for the study of nutrient dynamics in the future. A reasonable next step toward that would be to perform a similar test with a filamentous fungus, and if successful, incorporate a plant into the experiments as well.

I also attempted to replicate protocols from previous papers. In the end, we had to acknowledge that some of them simply do not work. In this respect, one of the key lessons is that anyone developing a new protocol or method should pay the utmost attention on carefully documenting everything they did. In several cases (Pandit et al., 2019; Whiteside et al., 2009) we set forth to replicate something and were immediately faced with lots of questions that were not answered in the text

or supplementaries, nor by the authors, despite several inquiry attempts. Replicability is one of the hallmarks of the scientific method, which is why it is worrying how impossible many published studies are to replicate. Such problems in replicability have previously been observed in several other fields in what has been termed as the "Replication crisis" (M. Baker, 2016). This lack of accurate reporting and stating of methodological limitations, as well as the unwillingness of authors to answer questions about their work (Gabelica et al., 2022), increases the chances of the spread of misinformation and unjustified conclusions and may ultimately lead to methodological crises, like the one that has recently unfolded in relation to the CMNs and isotopes (Henriksson et al., 2023, Karst et al., 2023).

In paper **II**. we employed DNA metabarcoding in a more traditional ecological study, with the aim to assess the effect of tree genotype on the fungal communities that they harbour. Although the method is already well established (Tedersoo et al., 2022), our experimental set-up enabled us to use it to gain novel results. Our knowledge on how intraspecific genetic variation of plants affects their fungal symbionts has so far been limited, and most previous studies include no replicates of plants of the same genotype. Thus, the utilization of micro propagated clonal trees in our study enabled a more robust analysis of genotype effects. The obtained results indicated that plant individuals may differ in their ability to accumulate fungal taxa to their roots. This could have implications to the survival and fitness of the trees, as the abundance and diversity of root fungal taxa may reflect on related benefits, such as nutrient accusation ability, stress tolerance and resistance to pathogens (Wagg et al., 2011). Although studies in more natural environments are needed to corroborate these findings, they show that the effect of host genotype on community assembly of root fungi may extend beyond species level effects. In fact, the effect of genotype could be even stronger in natural forests, where the species pool of ectomycorrhizal (EM) taxa is likely much richer than it was in the common garden field, which has previously harboured mostly AM plants. It has also been shown that site disturbance and urbanization can homogenize the fungal species pool (Abrego et al., 2020). Indeed, our samples were rich in generalist fungi often found in disturbed and urban soils, and these fungi are likely much less responsive to host genotype effects than many EM fungi found in natural forests. In that case, there could be yet another factor increasing the complexity of CMNs, because resource transfer might differ not only due to genetic differences between plant species but due to genetic differences in individual plants as well. Indeed, the mapping and study of tree genotypes and their related CMNs has been highlighted as one of the important aspects to be explored in future studies (Karst et al., 2023). Thus, DNA metabarcoding as well as other genetic approaches have the potential to compliment the study of CMNs in the future.

Like the more established metabarcoding method, isotopic methods have, and can still yield new information on interplant nutrient transfer, even if fully ruling out all alternative pathways is not possible. It has already been argued that although some label movement through alternative pathways likely occurs, large amounts of label cannot move from plant to plant without CMNs (Klein et al.,

2023). Furthermore, it must not be forgotten that our knowledge on mycoheterotrophic and mixotrophic plants, including orchid mycorrhizal plants, is largely based on isotope experiments (Courty et al., 2011; Lerat et al., 2002; McKendrick et al., 2000; Selosse & Roy, 2009). There are also other counter points being raised in favour of isotopic methods and the obtained results in relation to common mycorrhizal networks (Klein et al., 2023). Among these, the complexity of the CMNs and plant root systems connected to them has been suggested as a possible culprit for observed lack of transfer. Seeing how much my experiments with FNPs were hindered by the complexity of this system, it is not impossible that the same complexity has hindered the observation of the isotopic labels as well.

As no method is perfect, the theoretical best way to approach any research problem would probably be the use of multiple methods and experiments that complement each other. In the case of CMN nutrient transfer, this might mean a combination of quantum dots containing isotopically labelled nutrients, control treatments with isotopes and quantum dots combined with all relevant controls for each method, and metabarcoding or molecular genetics analysis to confirm the presence of the same fungal genets in the roots of the studied plants. Indeed, a study comparing tracking with isotopes and FNPs has already been called for (Raven, 2022). In practice though, setting up such experiments would likely be very difficult, as they would require a big investment as well as numerous collaborators from various areas of science. No matter how hard one tries, it is not possible to plan these kinds of complex experiments with every parameter being optimal, as what is optimal from one perspective (e.g., anoxic conditions to minimize oxidation of certain functional groups in a molecule) may negatively affect another aspect (e.g., living plants and fungi).

Karst et al. (2023), have also given some suggestions for future studies. Many of these involve additional tests and treatments to be added to previously used experimental set-ups. These recommendations call not only for the proper exclusion of alternative pathways, but also for inclusion of additional parameters, such as pathogens, genetics, and site history to the investigations (Karst et al., 2023). Doing so will inevitably increase the level of complexity of the system and the experiments even further. Among the suggestions is also the use of novel methods, such as FNPs (Karst et al., 2023). However, based on our results, we are still extremely far from being able to utilize FNPs in these kinds of experiments. Thus, while it is true that FNPs might be helpful, it is clear that answering these questions is currently more feasible with the already established methods. Regardless, this will take considerable time and effort from the scientific community.

Despite my best efforts, the existence and significance of CMN nutrient transfer remains as unclear as it was before the start of this project, but it is clear that there is no magic method for studying this topic. Yet, the ongoing conversation on CMNs brings hope that more answers to this question are coming. More research on the topic, including the development of old and new methods, is bound to follow (Karst et al., 2023). As such, this thesis should be approached as another contribution to the CMN discussion in terms of methods. Hopefully, it prompts more investigation on the interactions of FNPs and fungi, more appreciation for the established methods and the results they may provide, and above

all, careful reporting of methodological details and their potential limitations (Henriksson et al., 2023). An important thing to remember in this conversation is also that *whether* such transfer occurs and *why* such transfer occurs are two different questions (Henriksson et al., 2023), and answering them may not be possible with the same method. For example, the transfer of a label alone, whether it be isotopic or fluorescent, does not confirm that the drivers of the transfer are altruistic, nurturing trees. Indeed, several studies have argued that mycorrhizal fungi are the true drivers of interplant transfers via CMNs (Lekberg et al., 2010; van't Padje, Werner, et al., 2020). Therefore, it is possible that fungi are extracting nutrients from one plant and transporting them to another plant that is allocating more carbon to them, while the "donor" plant is simply not stopping it. Indeed, it has been hypothesised that what has been observed as interplant carbon transfer, is actually the transfer of nutrient compounds, such as amino acids, which include carbon by necessity (Klein et al., 2023; Simard et al., 2012). Furthermore, many studies have reported that CMNs had adverse effects to the plants involved (Carey et al., 2004; Henriksson et al., 2023; Karst et al., 2023; Kytöviita et al., 2003; Merrild et al., 2013). Thus, it is likely that the drivers of the potential transfers would be dynamic and circumstantial. Indeed, evidence of dynamicity of transfer from individual plants to fungi and fungi to individual plants is strong (Hoeksema et al., 2010; Kiers et al., 2011; van't Padje, Oyarte Galvez, et al., 2020). Therefore, it is important to avoid oversimplification of conclusions drawn about CMNs and to respect the complexity of these systems, the unique challenges they pose, and the lack of understanding that we still have of them.

CONCLUSIONS

This thesis synthesizes insights from diverse scientific methodologies to investigate plant-fungal interactions, especially in the frame of common mycorrhizal networks (CMN). The current narrative on CMN function and significance, as well as the traditionally used isotopic labelling method, have received a lot of critique, and fluorescent nanoparticles (FNPs) have been suggested as a potential option to circumvent the problems associated with isotopic studies. In this thesis, a theoretical (**I.**) and practical (**III.**) assessment of the suitability of FNPs for such purposes has been assessed. We conclude that despite the apparent theoretical potential of FNPs (**I.**), and their demonstrated usefulness in answering many unique questions in biology (**I.**), their application in complex experiments of even more complex systems like CMNs is currently not realistic (**I.**, **III.**, unpublished data). FNP interactions with fungi and soil are largely unexplored (**I.**) and may be unpredictable (**III.**, unpublished data). Conversely, traditional methods, such as isotopic labelling, are currently more suited for CMN investigations. The results from paper **II.** Indicate that host tree genotypes may differ in their abilities to interact with root fungi. This may have implications for the growth and survival of tree individuals. It may also suggest that tree genotypes should be considered more closely when studying plant-fungal interactions, including CMNs. Thus, future studies on CMNs may benefit from the incorporation of metabarcoding approaches, such as those employed in paper **II.** Regardless of the tools chosen, the correct and thorough reporting of methods and their limitations is crucial. Based on the data obtained in papers **II.** and **III.** hypothesis 1. (trees from different origins harbour different root fungal communities) 3. (yeast cells take up FNPs only when connected to a nutrient source) and 4. (CQDs are more biocompatible than Cd containing QDs) were not supported. Conversely, hypothesis 2. (individual trees differ in terms of their root fungal communities) was partially supported by the data. Further studies are needed and expected in this field and the development of old and novel methods remains paramount. The current thesis may serve as an important reminder that a novel technique is not automatically superior to the old ones and may come with unexpected challenges.

SUMMARY

Soil ecosystems and microscopic organisms inhabiting them are an integral part of our planet and key providers of several ecosystem services related to the global carbon and nutrient cycles as well as food and timber production. Many soil organisms live in close connection with plant roots, which provide a direct link between aboveground and belowground ecosystems. Furthermore, plant roots are thought to be linked to each other via mycorrhizal fungi growing in their roots. The benefits of mycorrhizal symbiosis *per se* are well documented as fungi aid plants in nutrient accusation and stress and pathogen tolerance while the plants provide the fungi with photosynthetically produced sugars, which they use for growth. However, the extent and significance of the mycorrhizal plant-to-plant linkages, referred to as common mycorrhizal networks (CMNs), is highly debated.

The popularized narrative of CMNs entails that forest trees are connected to a vast network of fungal mycelium, which enables them to transfer resources, including carbon, nutrients, water, defence signals and allelochemicals, to each other and therefore support each other in a communal manner. However, critics of this narrative attain that the evidence are lacking, largely due to the limitations of the isotopic labelling methods utilized to study CMNs. Indeed, several landmark papers related to CMN resource transfer fail to acknowledge the possibility of resource transfer via pathways other than CMNs, such as root grafts, root exudates or diffusion through soil. Control treatments involving meshes of different pore sizes, rotating growth cores, air gaps and trenching, have been utilized in an attempt to account for the limitations of this method, especially the alternative transfer pathways. However, it has been argued that none of the treatments may be used to fully overcome the issues of isotopic labelling. Furthermore, the low spatial accuracy of the isotope labelling method does not enable the separation of isotopes inside plant roots from isotopes contained within fungal tissues in and around the roots. However, the ecological significance of the observed transfer is vastly different depending on whether the isotopes enter plant tissues or not. Thus, the improvement of existing methods and the development of new ones is instrumental for obtaining concrete answers to the open questions about CMNs.

The use of fluorescent nanoparticles (FNPs), microscopic particles that produce fluorescence upon light excitation, has been suggested as a potential alternative method for studying CMN resource transfer. The major benefit of FNPs compared to isotopes is that their movement can be observed in real-time, in vivo. This entails that the pathway of nutrient movement and their precise localisation in tissues can be visually confirmed. This contrasts with isotopic approaches, that only allow measurements of transferred isotope in the main plant organs after the transfer has taken place. Although FNPs have been widely used in technical and medical applications, practical experiments with FNP and fungi are rare. Thus, their theoretical and practical suitability for CMN research is uncertain.

The purpose of this thesis was to determine the theoretical and practical suitability of different types of FNPs for the study of plant-fungal interactions, especially CMNs. The first paper (**I.**) comprises a comprehensive review on previous bio experiments utilizing FNPs. It highlights the potential of the particles for various biological applications, including the study of CMNs, while critically evaluating the technique, its limitations, and future developmental needs. Different particle types are also introduced and compared. The reviewed literature reveals that the most commonly used type of FNP in biological studies are CdSe/ZnS quantum dots. However, as these particles contain the hazardous heavy metal cadmium, their use in biological experiments, especially long-term, has been questioned. A promising newer alternative to cadmium containing QDs are carbon quantum dots (CQDs), which are expected to be more biocompatible due to their more natural composition. However, these particles suffer from the lack of available data, protocols and standardization. Nonetheless, the previous studies highlight the theoretical potential of this technique.

The third paper (**III.**) builds on the information on the review paper and features an experimental proof-of-concept study of the toxicity and interactions of two types of FNPs, commercial CdSe/ZnS quantum dots and self-synthesised carbon quantum dots, with yeast cells. The obtained results, as well as previous experimental attempts of ours, highlight the lack of knowledge we still have on FNP interactions with plants, fungi and soil. Indeed, most previous studies have been performed on animal cells, which lack cell walls that can hinder the entry of nanoparticles to cells. We observed that contrary to common assumptions, Cd containing FNPs did not induce toxic effects. However, they were also not taken up by fungal cells, likely due to their large aggregate size. Conjugation with the amino acid cysteine did not affect the uptake of CdSe/ZnS QDs, as both pristine and conjugated QDs only loosely adsorbed to the surfaces of yeast cells. Furthermore, washing of the cells detached the QDs from the cells, indicating weak and passive interactions. Contrastingly, the smaller carbon containing FNPs readily entered fungal cells, and were observed there even after washing of the cells. Thus, the tested carbon FNPs show potential for future applications related to fungi. However, due to the considerable gap between our knowledge on FNPs and the complexity of CMNs, previously used methods are currently more suited to the study of CMNs. Moreover, the utility of FNPs in the study of plant-fungal resource transfer has recently been questioned, because although small, FNPs are much larger than free nutrients, and are thus likely to be taken up by different transfer pathways than free nutrients. Therefore, the movement of FNP-conjugated nutrients may not accurately mimic natural nutrient movement.

In parallel with the FNP studies, we also published a study (**II.**) on plant-fungal interactions utilizing the more established DNA metabarcoding method. In this study, clonal birch trees originating from different latitudes were grown together in a common garden, and the effect of tree genotype on root fungal communities was assessed. Previous studies on genotype effects on fungal symbionts have suffered from a lack of clonal replicates of genotypes. In this respect, our study enabled a more robust exploration of genotype effects. The results showed that trees of different genotype differed in the abundance and diversity of fungi

in their roots, which indicates that tree individuals may have different abilities to select for the fungi that inhabit their roots. Such differences might affect the competitive abilities of the plants, as the abundance and diversity of root symbionts may reflect on related benefits. In light of this, tree genotypes may have an effect on the dynamics of CMN resource transfer, not only on the level of species, but also on the intraspecific level. Indeed, due to the complexity of the CMNs, their robust study requires complex experimental set-ups that include several control treatments and account for a multitude of different factors.

This thesis is a contribution to the active discussion on the study of CMNs and the methods for studying them. There is no simple solution to the challenges that CMN studies entail, but the continued development of methods remains integral also in the future. A combination of various methods, including FNPs, isotopes and DNA-based techniques may be necessary. However, no matter the method used, there are always potential confounding factors that cannot be excluded. Thus, the correct reporting of methods used, as well as clear disclosure of their potential limitations, is fundamental. Issues related to poor replicability of previous studies and the unwillingness of authors to answer questions about their publications hindered the progress of this PhD project and may affect the spread of misinformation on scientific results in a broader sense.

In the two experimental studies, we set forward four hypotheses. With regards to the DNA metabarcoding study on birch trees, we hypothesised that 1. root fungal communities of trees of different origin would differ and 2. root fungal communities of individual trees would differ. Based on our data, hypothesis 2. was partially supported, as the within group variation and OTU accumulation between genotypes differed. The proof-of-concept study with FNPs and yeasts was executed with the aim to test two additional hypotheses. Hypothesis 3. assumed that FNPs would enter fungal cells only when connected to a nutrient source. The final hypothesis (4.) was that FNPs with a carbon core would be more suited to fungal tracking than Cd-containing QDs, due to their better biocompatibility. Neither hypothesis 3. or 4. were supported by the experimental data, highlighting how little we still know about the interactions of FNPs with fungal cells.

SUMMARY IN ESTONIAN

Taimede ja seente interaktsioonide uurimismeetodid: pilguheit minevikku, olevikku ja tulevikku

Mullaökosüsteemid ja neid asustavad mikroskoopilised organismid on meie planeedi lahutamatu osa ning mitmete globaalsete süsiniku- ja toitaineteringlusega ning toidu- ja puidutootmisega seotud ökosüsteemiteenuste peamised pakkujad. Paljud mullaorganismid elavad tihedas ühenduses taimede juurtega, mis loovad otsese seose maapealsete ja maaaluste ökosüsteemide vahel. Lisaks arvatakse, et taimede juured on üksteisega seotud nende juurtes kasvavate mükoriisaseente kaudu. Mükoriisse sümbioosi eelised on hästi dokumenteeritud, kuna seened aitavad taimi toitainete omandamise ning stressi- ja patogeenitaluvusega, samas kui taimed varustavad seeni fotosünteesi teel toodetud suhkrutega, mida nad kasutavad kasvamiseks. Siiski vaieldakse tugevalt mükoriisa taimedevaheliste sidemete ulatuse ja olulisuse üle – seda nimetatakse mükoriisavõrgustikuks (i.k. common mycorrhizal network – CMN).

CMN-ide populariseeritud narratiiv eeldab, et metsapuud on ühendatud tohutu seeneniidistiku võrgustikuga, mis võimaldab neil ressursse, sealhulgas süsinikku, toitaineid, vett, kaitsesignaale ja allelopaatilisi ühendeid , üksteisele üle kanda ja seega üksteist kogukondlikult toetada. Selle narratiivi kriitikud leiavad aga, et tõendid puuduvad peamiselt CMN-ide uurimiseks kasutatavate isotoopmärgistusmeetodite tehniliste piirangute tõttu. Tõepoolest, mitmed CMN-i ressursside ülekandmisega seotud olulised uuringud ei tunnista ressursside ülekandmise võimalust muude võimaluste kui CMN-ide kaudu, näiteks juurepoogid, juureeritised või difusioon läbi pinnase. Selle meetodi piirangute, eriti alternatiivsete ülekandevõimaluste piirangute arvestamiseks, on kasutatud kontrolltöötlusi, mis hõlmavad erineva poorisuurusega võrke, pöörlevaid kasvusüdamikke, õhupilusid ja juurte läbikaevamist. Siiski on väidetud, et ühtegi meetodit ei saa kasutada isotoopmärgistusega seotud probleemide täielikuks lahendamiseks. Lisaks ei võimalda isotoopide märgistamise meetodi madal ruumiline täpsus eraldada taimede juurtes olevaid isotoope juurte sees ja nende ümber olevates seenekudedes. Täheldatud ülekande ökoloogiline tähtsus on aga suuresti erinev sõltuvalt sellest, kas isotoobid sisenevad taimekudedesse või mitte. Seega on olemasolevate meetodite täiustamine ja uute väljatöötamine abiks konkreetsete vastuste saamiseks CMN-ide kohta.

Võimaliku alternatiivse meetodina CMN-i ressursside ülekande uurimiseks on soovitatud kasutada fluorestseeruvaid nanoosakesi (i.k. fluorescent nanoparticles – FNP), mikroskoopilisi osakesi, mis tekitavad valgusega ergastamisel fluorestsentsi. FNP-de peamine eelis võrreldes isotoopidega on see, et nende liikumist saab jälgida in vivo reaalajas. See tähendab, et toitainete liikumise teed ja nende täpset paiknemist kudedes saab visuaalselt kinnitada. See on vastuolus isotoopmeetoditega, mis võimaldavad mõõta ülekantud isotoopi peamistes taimeorganites alles pärast ülekande toimumist. Kuigi FNP-sid on tehnilistes ja meditsiinilistes rakendustes laialdaselt kasutatud, on praktilised katsed FNP-de ja

seentega haruldased. Seega on nende teoreetiline ja praktiline sobivus CMN-uuringuteks ebakindel.

Käesoleva lõputöö eesmärk oli välja selgitada erinevat tüüpi FNP-de teoreetiline ja praktiline sobivus taim-seen interaktsioonide, eriti CMN-ide uurimiseks. Esimene artikkel (I.) sisaldab põhjalikku ülevaadet varasematest biokatsetest, milles kasutati FNP-sid. See tõstab esile osakeste potentsiaali mitmesugustes bioloogilistes rakendustes, sealhulgas CMN-ide uurimisel, hinnates samal ajal kriitiliselt uurimismetoodikat, selle piiranguid ja tulevasi arenguvajadusi. Samuti tutvustatakse ja võrreldakse erinevaid osakeste tüüpe. Kirjandusest selgub, et bioloogilistes uuringutes kõige sagedamini kasutatav FNP tüüp on CdSe / ZnS kvantpunktid (QD). Kuna need osakesed sisaldavad aga ohtlikku raskemetalli kaadmiumi, on nende kasutamine bioloogilistes katsetes, eriti pikaajalistes, kahtluse alla seatud. Paljutõotav uuem alternatiiv kaadmiumi sisaldavatele kvantpunktidele on süsiniku kvantpunktid (CQD), mis on eeldatavasti nende naturaalsema koostise tõttu bioühilduvamad. Need osakesed kannatavad aga kättesaadavate andmete, protokollide ja standardimise puudumise tõttu. Sellegipoolest rõhutavad varasemad uuringud selle tehnika teoreetilist potentsiaali.

Kolmas artikkel (III.) põhineb esimese artikli (I.) teabel ja sisaldab eksperimentaalset kontseptsiooniuuringut kahte tüüpi FNP-de, kaubanduslike CdSe / ZnS kvantpunktide ja ise sünteesitud süsiniku kvantpunktide toksilisuse ja koostoimete kohta pärmirakkudega. Saadud tulemused, nagu ka meie varasemad eksperimentaalsed katsed, rõhutavad teadmiste puudumist, mis meil endiselt on FNP koostoimete kohta taimede, seente ja pinnasega. Tõepoolest, enamik varasemaid uuringuid on tehtud loomarakkudega, millel puuduvad rakuseinad, mis võivad takistada nanoosakeste sisenemist rakkudesse. Täheldasime, et vastupidiselt tavalistele eeldustele ei põhjustanud FNP-sid sisaldav Cd toksilist toimet. Kuid need osakesed ei sisenenud ilmselt agregaadi suuruse tõttu seenerakkudesse. Konjugatsioon aminohappe tsüsteiiniga ei mõjutanud CdSe/ZnS kvantpunktide omastamist, kuna nii põlised kui ka konjugeeritud kvantpunktid adsorbeerusid ainult lõdvalt pärmirakkude pindadele. Lisaks eraldas rakkude pesemine kvantpunkte rakkudest, mis näitab nõrka ja passiivset interaktsiooni. Vastupidiselt sisenesid väiksemad süsinikku sisaldavad FNP-d kergesti seenerakkudesse ja neid täheldati seal isegi pärast rakkude pesemist. Seega näitavad testitud süsiniku FNP-d potentsiaali seentega seotud tulevaste rakenduste jaoks. Kuid kuna meie teadmistes FNP-de ja CMN-ide keerukuse vahel on märkimisväärne lõhe, sobivad varem kasutatud meetodid praegu CMN-ide uurimiseks paremini. Veelgi enam, hiljuti on kahtluse alla seatud FNP-de kasulikkus taimede ja seente ressursside ülekande uurimisel, sest kuigi FNP-d on väikesed, on need palju suuremad kui vabad toitained ja seega võetakse need tõenäoliselt kasutusele erinevatel ülekandeteedel kui vabad toitained, mistõttu ei pruugi FNP-ga konjugeeritud toitainete liikumine täpselt jäljendada loomulikku toitainete liikumist.

Paralleelselt FNP uuringutega avaldasime ka uuringu (II.) taimede ja seente interaktsioonide kohta, kasutades väljakujunenud DNA-põhise määramise meetodit. Antud uuringus kasvatati samal uuringualal koos erinevatelt laiuskraadidelt pärit kase kloone ning hinnati puude genotüübi mõju juureseente kooslustele. Varasemad uuringud genotüübi mõju kohta seente sümbiontidele on kannatanud

genotüüpide replikatsioonide puudumise tõttu. Meie uuring võimaldas genotüübi mõju põhjalikumalt uurida. Tulemused näitasid, et erineva genotüübiga puud erinevad seente arvukuse ja mitmekesisuse poolest oma juurtes, mis viitab sellele, et puuisenditel võib olla erinev võime selekteerida oma juuri asustavaid seeni. Sellised erinevused võivad mõjutada taimede konkurentsivõimet, kuna juursümbiontide arvukus ja mitmekesisus võivad peegeldada seotud eeliseid. Selle valguses võivad puude genotüübid avaldada mõju CMN-i ressursside ülekande dünaamikale mitte ainult liikide, vaid ka liigisisesel tasandil. Tõepoolest, CMN-ide keerukuse tõttu nõuab nende uurimine keerulisi eksperimentaalseid seadistusi, mis hõlmavad mitut kontrollkäsitlust ja võtavad arvesse paljusid erinevaid tegureid.

Antud doktoritöö on panus aktiivsesse arutelusse CMN-ide uurimise ja selle metoodika üle. CMN-uuringutega kaasnevatele väljakutsetele lihtsat lahendust ei ole, kuid meetodite jätkuv arendamine on oluline ka edaspidi. Vajalik võib olla erinevate meetodite, sealhulgas FNP-de, isotoopide ja DNA-põhiste tehnikate kombineerimine. Kuid olenemata kasutatavast meetodist on alati võimalikud segavad tegurid, mida ei saa välistada. Seega on kasutatud meetodite täpne aruandlus ja nende meetodite võimalike piirangute selge avalikustamine üliloluline. Varasemate uuringute halva korratavusega seotud probleemid ja autorite soovimatus vastata oma publikatsioone puudutavatele küsimustele takistasid käesoleva doktoritöö edenemist ning võivad ka üldisemalt mõjutada teadustulemuste kohta laiemalt leviva valeinformatsiooni levikut.

Kahes eksperimentaalses uuringus esitasime neli hüpoteesi. Kaskede juureseente DNA-põhise määramise uuringu osas püstitasime hüpoteesi, et 1. erineva päritoluga puude juurekooslused erinevad ja 2. üksikute puude juurte seenekooslused erinevad. Meie andmetele tuginedes leidis hüpotees 2. osaliselt toetust, kuna grupisisene variatsioon ja OTU akumulatsioon genotüüpide vahel erinesid. Kontseptsiooni tõestamise uuring FNP-de ja pärmidega viidi läbi eesmärgiga testida kahte täiendavat hüpoteesi. Hüpotees 3. eeldas, et FNP-d sisenevad seenerakkudesse ainult siis, kui need on ühendatud toitaineallikaga. Lõplik hüpotees (4.) oli, et süsiniku tuumaga FNP-d sobivad paremini seente jälgimiseks kui kaadmiumi sisaldavad kvantumpunktid, kuna need on parema bioloogilise sobivusega. Eksperimentaalsed andmed ei toetanud hüpoteese 3. ega 4. See tõi esile, kui vähe me veel teame FNP-de koostoimest seenrakkudega.

ACKNOWLEDGEMENTS

I of course wish to thank everyone who has helped me in one way or another to manage this far. Supervisors: Leho Tedersoo, Raivo Jaaniso and Uno Mäeorg; colleagues, coauthors, and friends. From the mycology work group, I am especially thankful to Jane Oja, Heidi Tamm, Niloufar Hagh Doust, Vladimir Mikryokov, Olesya Dulia and Iryna Yatsiuk. You have been my colleagues and will remain my friends. I also thank Dr. Djuddah Leijen and the Communicating Science course crew, for giving me a valid excuse to leave the mycology bubble occasionally. I owe a special thank you to my mentor Sari-Kontunen Soppela, for her constant support even though she had no obligation to continue it after I left UEF. I am also grateful to everyone at KBFI who took me to their lab and cared about my project. The biggest thanks of all go to my husband Toivo for putting up with my complaining and my dog Tilke for giving me a reason to smile no matter how bad things seemed.

Acknowledgement is also given to all the funders that have enabled me to try to be a scientist and produce the experiments for my publications. These include Estonian Research Council grants PRG749, STP28, PRG632, MOBERC45, EMP442, Academy of Finland project 138309 and strategic funding of University of Eastern Finland (project 931060) and Societas Biologica Fennica Vanamo.

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Färkkilä S. M. A., Valtonen A., Saravesi K., Anslan S., Markkola A., Kontunen-Soppela S., 2023. The effects of geographic origin and genotype on fungal diversity of silver birch (*Betula pendula*), Fungal Ecology 63, 101241. https://doi.org/10.1016/j.funeco.2023.101241

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DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
3. **Kristjan Zobel**. Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
4. **Andres Mäe**. Conjugal mobilization of catabolic plasmids by transposable elements in helper plasmids. Tartu, 1992, 91 p.
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