Mycorrhizas and biomass crops: opportunities for future sustainable
development

Deirdre C. Rooney¹, Ken Killham², Gary D. Bending³, Elizabeth Baggs², Martin
Weih⁴ and Angela Hodge¹

¹Department of Biology, University of York, Area 14, PO Box 373, York, YO10
5YW, UK
²Institute of Biological and Environmental Sciences, Cruickshank Building, St.
Machar Drive, Aberdeen, AB24 3UU, UK
³Warwick HRI, University of Warwick, Wellesbourne, Warwick, CV35 9EF, UK
⁴Department of Crop Production Ecology, Box 7043, 750 07, Uppsala, Sweden

Corresponding author: Rooney, D.C. (deirdre.rooney@askham-bryan.ac.uk)
Abstract

Central to soil health and plant productivity in natural ecosystems are in situ soil microbial communities, of which mycorrhizal fungi are an integral component, regulating nutrient transfer between plants and the surrounding soil via extensive mycelial networks. Such networks are supported by plant-derived carbon and are likely to be enhanced under coppiced biomass plantations, a forestry practise that has been highlighted recently as a viable means of providing an alternative source of energy to fossil fuels, with potentially favourable consequences for carbon mitigation. Here, we explore ways in which biomass forestry, in conjunction with mycorrhizal fungi, can offer a more holistic approach to addressing several topical environmental issues, including ‘carbon-neutral’ energy, ecologically sustainable land management and CO₂ sequestration.

Sustainable biomass production for future energy needs

Current developments in agriculture have involved growing bioenergy crops on agricultural land, with a shift in focus from yield- and quality-related issues towards more sustainable forms of agriculture [1]. A major challenge facing global bioenergy production is striking the balance between long-term sustainability, and reaching short-term productivity goals if bioenergy is to become a viable means of reducing fossil fuel dependency. ‘Sustainability’ in agriculture is difficult to define unequivocally, but often involves minimal chemical inputs, efficient nutrient recycling and enhancement of important microbial-driven processes such as nutrient acquisition, decomposition and protection against pathogens. Perennial crops, such as Salix (willow) and Populus (poplar) species, grown in short rotation coppice (SRC) biomass plantations represent an interesting opportunity to promote
agricultural sustainability, by enhancing regulation of important ecological processes [1]. Although willow SRC is commercially grown in several countries including Sweden (~14000 ha), the production of biomass for energy from SRC forestry is still in the experimental stages of development in major countries such as the UK and US [2]. Land availability and biomass yield are major concerns surrounding biomass as an energy source [3-7], yet the contribution of biomass derived energy to global renewable energy stocks (~50% in 2004) remains significant [8].

Less attention, however, has focussed on sustainable SRC culture, including interactions with soil microbial communities. As primary producers, plants provide photosynthetically derived carbon to the soil microbial community, including symbiotic mutualists, decomposers and pathogens [9] via rhizodeposition [10] which is easily assimilated by the soil microbial biomass [11,12]. A vital component of the soil microbial community, mycorrhizal fungi, represent the primary interface between photosynthate and soil through intimate associations with plant roots, and have a central role in plant nutrient acquisition and plant health [13]. Interestingly, the perennial nature of SRC crops is associated with minimal mechanical disturbance of soil and is likely to promote belowground mycorrhizal functioning which, in turn, could promote biomass yield and cropping security. Compared with conventional cropping systems, SRC plantations are only replanted every 10-25 years (depending on national regulation, market issues and plantation health), which significantly lengthens crop-rotation periods and the crop is generally more deeply-rooted, requiring no annual soil cultivation or herbicide application once established (Box 1). In addition, considerably less agrochemical inputs, in particular nitrogen, are required in SRC. Non-intensive management of
SRC plantations may also present significant potential for belowground carbon sequestration [14,15], which can improve soil quality in SRC (Box 2). Carbon sequestration is especially relevant to renewable energy production as it represents an additional carbon offset compared with fossil fuel emissions.

Understanding plant-microbial interactions is crucial to our understanding of soil ecosystem function and its role in sustainable land management. Here we discuss the potential importance of interactions between mycorrhizas and biomass crops in SRC systems, with particular reference to the sustainable generation of biomass for renewable energy and the potential for carbon sequestration.

**Mycorrhizas in biomass crop plantations**

Mycorrhizal fungi are an important integral component of the plant-soil system, forming symbiotic associations with most land plants and mediating a range of crucial ecosystem processes [13,16]. In return for photosynthetically derived carbon, mycorrhizal fungi have a fundamental role in plant nutrition, most notably in the provision of phosphorus and nitrogen to the host plant [13]. In addition, other non-nutritional benefits, such as soil aggregation and stability [17], increased drought tolerance, and protection against pathogens [18, 19] can be conferred upon the associated host. Although mycorrhizas have been found associated with several biomass-producing plant species, such as *Populus* and *Salix* species [20-25], information concerning their functional role in SRC plantations is scarce.

Two major types of mycorrhizal fungi, the arbuscular mycorrhizal fungi (AMF) and the ectomycorrhizal fungi (ECMF), form symbiotic associations with most land plants. AMF (~200 species described) are likely to have coevolved with
terrestrial plants, at least partially facilitating the colonisation of land by plants over 400 million years ago [26] and can form associations with approximately two-thirds of land plants. ECMF (~6000 species described) are likely to have evolved later (130 million years ago) and are generally associated with woody plants [13]. Both AMF and ECMF support extensive extraradical hyphal networks maintained by plant-fixed carbon (Figure 1), which act as a conduit for nutrient exchange between plant roots and the soil environment. Interestingly, the main tree genera used in biomass plantations worldwide (Salix, Populus and Eucalyptus) can form both AMF and ECMF associations, occasionally with AMF and ECMF present in the same root system [27]. Such ‘dual-colonisation’ can result from several factors, including successional stages in tree development (as the tree matures and the root develops) [28], availability of mycorrhizal inoculum strength (availability of fungal spores and/or hyphal fragments) [25], local soil conditions [13] or geographical location [29]. It is possible that different mycorrhizal types or species associated with a given plant could offer functional complementarity (see Glossary) [30]. However, although dually-colonised trees in SRC plantations have been reported [23,25,27,31], it is usually one type of mycorrhizal association that dominates or exclusively colonises a given plant at any one time. Studies of willow plantations revealed ECMF as the dominant mycorrhizal association, with AMF accounting for significantly lower root colonisation, often <1% [20,23-25,31]. Similarly, ECMF, rather than AMF, dominated both willow and poplar stands on afforested sites in Northern Germany [32].

Growth and maintenance of mycorrhizal structures is supported by plant-fixed carbon, and establishment of mycorrhizal symbioses therefore comes at a carbon ‘cost’ to the plant. Extraradical (outside the root) hyphal growth is often
extensive and can account for up to 30% of the microbial biomass in soil [33,34]. Plant investment in mycorrhizas is offset by the benefits gained (such as increased nutrient acquisition) in most cases, hence mycorrhizal associations are considered mutualistic. In fact, plant investment in mycorrhizal hyphae ‘cost’ the plant 100 times less carbon to construct a unit of hypha than it would that of a root [35], effectively making the symbiosis cost-effective in terms of plant carbon investment, especially as hyphae can extend beyond the nutrient depletion zone that develops around the roots. Plant investment in mycorrhizas should therefore decline as soil nutrient availability increases, as an abundance of labile nutrients (such as fertiliser additions) reduces the need for a foraging symbiont. However, the sparse experimental evidence for nutrient fertilization effects on mycorrhizal colonization of SRC crops indicates variable relationships: fertilization either reduced or increased mycorrhizal colonisation of SRC willow, depending on soil and/or other site-specific conditions [20]. Increased understanding about the relationships between soil nutrient availability and mycorrhizal colonisation in SRC could be used to develop marginal land for SRC forestry, thus reducing competition for high-quality agricultural land, which is increasingly in demand to fulfil global food and housing requirements [36].

**The role of mycorrhizas in soil carbon cycling**

A main feature of mycorrhizal symbioses is carbon flux from the plant to the fungal symbiont, making mycorrhizas an integral link in global carbon cycling. Mycorrhizal colonisation alters the carbon metabolism of the plant, increasing the carbon allocation to the whole root system [37], with a significant proportion (4-20%) diverted to the fungal component [12,38,39]. $^{13}$CO$_2$ labelling experiments
have indicated that carbon translocation to fungal hyphae can be rapid (within 24 hr of fixation; [38]), although slower delivery rates of up to 4 days post-labelling have also been reported [40]. Poplar and willow species support substantial root systems, presumably with a significant proportion of fixed carbon allocated to the roots, which can be stored in the root system to support new shoot development following a coppicing cycle [41]. It is currently unknown how mycorrhizal carbon flux is altered during coppicing cycles, especially with regards to carbon allocation to the fungal component when the aboveground biomass is harvested. It is possible that coppicing causes the plant to initially retain its carbon store for self-regeneration, until there is ‘need’ to divert some to the fungal component (i.e. when mineral nutrients become limiting for growth).

Characteristic mycorrhizal exudates including amino acids, organic acids, sugars and polysaccharides have been identified [42-45] and can be quickly assimilated by the soil microbial biomass. Additionally, other fungal-specific exudates, such as glomalin (a fungal glycoprotein), are produced by AMF. Glomalin is highly persistent in soil (residence time of 4-62 yr) and acts as soil ‘glue’, which can improve soil structure by enhanced soil aggregation [46,47]. Qualitative and quantitative differences in mycorrhizal exudates might also contribute to soil chemical, physical and biological heterogeneity, creating hotspots of microbial activity and promoting soil activity. However, incorporation of recently fixed carbon into the soil microbial biomass represents only one route for the total diverted carbon, with a substantial carbon diversion to other fungal structures, particularly investment in the external mycelial network. Carbon turnover from fine AMF hyphae can be rapid (5-6 days) with thicker hyphae taking up to 30 days [48], thus representing an important pathway by which plant-assimilated carbon enters
the soil environment [49]. This is in contrast to root turnover, which can take several years depending on the root diameter and plant species [50]. Difficulties arise in attempting to apply these turnover times to all fungal tissues, however, especially if considering the carbon investment associated with the extraradical mycelial network or characteristic fungal structures. Intraradical vesicles, reproductive spores, arbuscules (in AMF), intra- and extraradical hyphae collectively consume a large fraction of carbon allocated to the fungus. This carbon pool is likely to have a much longer mean residence time in soil [51] than 5-6 days; an observation which is supported by data suggesting that the residence time of carbon in ECMF communities is 4-5 years [52]. Collectively, these data suggest that mycorrhizas contribute to short and long-term soil organic carbon pools [47, 51].

In terms of carbon sequestration, long-term belowground storage of plant-fixed carbon in stable organic forms derived from fungal spores and glomalin (the latter by AMF only) offers a means of carbon storage in a relatively stable form. Soil organic matter accumulation was shown to significantly increase in both willow and poplar biomass plantations in the six years following afforestation of arable sites, which was attributed to inputs from leaf and root litter from the newly established stands [32]. Additionally, this increase in organic matter content was implicated in the increased ECMF associations in the same willow and poplar plantations [32]. An interesting concept arising from biomass production is that of biochar generation. Biochar is a derivative of biomass carbon, formed when biomass is partially combusted (in the absence of oxygen) to generate energy. Such partial combustion typically releases ~50% of the carbon contained in the biomass and produces a carbon-rich powdery substance (biochar) as an end
product, which can be added back to the soil for long term storage. Biochar has the potential to sequester up to 40% of initial biomass carbon owing to its long residence time in soil (thousands of years) compared with complete combustion, which retains ~3% carbon, and decomposition, which can sequester only up to 20% carbon after ten years [53]. Biochar addition to soil can also have positive effects on mycorrhizal status, notably with increases in root colonisation [54]. The effects of biochar on mycorrhizas can be attributed to changes in soil physico-chemical factors, such as nutrient availability and microbial activity. The exact mechanisms governing mycorrhizal responses to biochar in soil require further investigation however, particularly with regards to ERM dynamics. Quantification of the contributions of biochar to soil carbon storage in SRC systems is also an important consideration for future energy production from biomass (Box 2).

**SRC, nutrient cycling and mycorrhizas**

Coppicing is practiced in forestry as a means of removing apical dominance to encourage accelerated growth and increased yields, and in SRC plantations coppicing typically occurs every 3-5 years [41]. Following coppicing, re-growth of new plant biomass is facilitated by the regeneration of new shoots from the remaining stump. Conventional land management practices often include tillage and significant inputs of nutrients, herbicides and pesticides can have negative impacts on the number of mycorrhizal species present and can, in effect, marginalise mycorrhizal and microbial functioning [19,55,56]. In commercial SRC culture, the use of herbicides is required only during establishment of the plantation and pesticide application is generally not required [57]. SRC plantations could therefore be managed organically after the establishment phase, as a total
absence of fertilisation could allow biomass yield to decline to economically unfeasible levels. Extrapolating these data to SRC biomass plantations is difficult however, as interactions with other site-specific variables can alter mycorrhizal dynamics in soil.

Preservation of soil microbiology in less intensively managed sites can contribute to self-regulation of fundamental ecosystem processes, particularly nutrient recycling, without need for further nutrient inputs. Given the support for mycorrhizal enhancement of plant nutrient status [13], however, the problem of nutrient limitation of yield can be alleviated by mycorrhizal retrieval of nitrogen and phosphorus from soil organic material. High-yielding perennial trees, such as those grown in biomass plantations, can generally produce high dry matter yields from modest nitrogen applications (20-50% less nitrogen fertilisation than annual crops) [41]. This may mean that nitrogen inputs to SRC plantations can often be kept to a minimum (at least compared to many conventional agricultural practices), thereby minimising the possibility of adverse environmental impacts which may ensue if excess nitrogen is applied to the land. Closure of major nutrients cycles, such as nitrogen cycling, is one of the most important factors in ecologically sustainable systems, as it lowers the amount of nitrogen leached out or lost in gaseous form.

Enhancing the availability of phosphorus and nitrogen to host plants is considered the most important function of mycorrhizas [13], and nutrient availability in sustainable systems is often dependent on mycorrhizal activity. Phosphorus is a major nutrient required by plants, although in soil it is usually present in very low concentrations [13], as soluble phosphorus is readily taken up by both plants and microbes. Investment in mycorrhizas therefore means that plants can indirectly access nutrients beyond the nutrient depletion zone of the roots via extensive
mycelial networks. Both AMF and ECMF can effectively forage for relatively insoluble forms of soil inorganic phosphorus, such as rock phosphate, iron phosphates and aluminium phosphates [13]. In addition, ECMF have a major role in recycling soil organic nitrogen and organic phosphorus which are unavailable to the plant. In some forests, ECMF can suppress the activity of saprotrophs, a process known as ‘the Gadgil effect’, whereby ECMF inhibition of saprotrophic microbes was implicated in reduced litter decomposition, allowing accumulation of organic matter in the soil [58]. This could have been due to ECMF being supplied with energy from their plant host, which could give them a competitive advantage over saprotrophs. Although it is not clear how these processes are regulated in SRC forests, these actions suggest a possible niche role for efficient nutrient cycling under low-input systems. By contrast, the role of AMF in retrieval of organic nitrogen is unclear as AMF are not known to have any saprotrophic capabilities, although AMF involvement in nitrogen capture from complex organic sources has previously been demonstrated in laboratory conditions [59,60].

Effects of mycorrhizas on soil biodiversity

Mycorrhizal persistence under sustainably managed SRC could promote soil biological diversity through further symbiotic interactions with important soil organisms. For example, specific bacterial groups often associate with mycorrhizal hyphae [61], including plant growth-promoting rhizobacteria (PGPR) [62,63] which are important contributors to overall plant growth and/or nutrition. In addition, some bacterial communities were shown to specifically attach to dead AMF hyphae, whereas others used exudates from living hyphae as a growth substrate, the latter including two known PGPRs (Pseudomonas fluorescens SBW25 and Paenibacillus
brailensis PB177) [64]. Mycorrhiza helper bacteria (MHB) have been identified as important components of both AMF and ECMF hyphospheres and are capable of increasing rates of mycorrhizal colonisation and suppressing soil pathogens [65]. A recent study demonstrated the effectiveness of introducing both selected mycorrhizal fungal and bacterial species to poplar seedlings at the nursery stage, where co-inoculation increased plant nutrient status and increased establishment success at various sites [66]. Furthermore, interactions with higher trophic organisms are enhanced by mycorrhizal presence, in particular hyphal predators such as collembolans, nematodes and mites [67,68], although little is currently known about the underlying mechanisms that govern these interactions. Hyphal grazing emphasises a further positive impact that mycorrhizas can have on soil food webs and soil biodiversity, the consequences of which might mean greater ecosystem productivity [69] and greater soil carbon storage. Difficulties are faced when attempting to extrapolate this sparse knowledge, derived mainly from microcosm work, to the field and specifically to SRC biomass plantations.

Another interesting example regarding the effects of mycorrhizas on higher trophic organisms is represented by the interactions between root mycorrhizal colonization and leaf herbivore resistance in willows [70]. In fact, mycorrhizas and their influence on crop resistance to phytophagous insects might involve a yet unexplored potential for the bioprotection of agricultural crops. Control of pests and diseases in biomass plantations is important for the maintenance of high yields (i.e. crop security). Plant resistance to insect attack is often mediated by tissue concentrations of phenolic compounds that affect insect behaviour, development and survival. In an experimental study, the effects of mycorrhizas on willow leaf chemistry were found to be dependent on specific combinations of fungal species
and plant genotype [70]. Mycorrhizal control over the production of plant foliar substances (e.g. salicylic acid) could therefore present opportunities for selection of compatible fungal and plant combinations to combat herbivory. In effect, this presents a conceptual basis for the development of biological control strategies against insect herbivory in willow and poplar biomass plantations.

**Challenges for future research**

The theoretical potential of bioenergy is vast, and considerable emphasis must be placed on conducting large-scale field trials to optimise biogeochemical conditions for sustainable biomass production. Many groups of organisms regulate essential ecosystem processes, but mycorrhizal fungi arguably represent the most important keystone group linking crop productivity and cropping security to below ground functioning (Figure 2). The preservation of mycorrhizal status in biomass plantations could significantly improve the viability of low-input SRC plantations. However, lack of information regarding the underlying functional relationships between plants, mycorrhizas, pests and microorganisms represents a major challenge in the attempt to achieve sustainability. We have identified the following areas which merit further investigation: the effects of mycorrhizas on biomass production and carbon sequestration under various management regimes; the effects of nutrient fertilization, regular harvests and biochar application on mycorrhizal functioning; the interactions between mycorrhizal fungal genotype and crop genotype. Another prerequisite for the successful implementation of sustainable management concepts into SRC culture is the consideration of ecological processes in crop breeding, as specific fungal – host genotype combinations seem to be crucial for the ultimate effects of mycorrhizas on crop
performance and pest resistance [70,71]. Resolution of such issues will contribute greatly to our understanding of how sustainable land management and future energy needs may be achieved.

Depletion of finite resources, such as global phosphate reserves, which are estimated to run out ~100-150 years from now, based on current exploitation rates [77, 78] suggests that management of organisms, such as mycorrhizal fungi, which can exploit and recycle soil phosphorus and nitrogen is advantageous. Integration of mycorrhizal systems with other carbon sequestration management practices, for example biochar usage [53,54] (Box 2), could also be an important future practice. The first mycorrhizal symbioses evolved over 400 million years ago in response to phosphorus deficiency in terrestrial ecosystems [35], and we suggest that capitalisation on this strategy in sustainably managed ecosystems could become essential for future land management and crop production.

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**Box 1. Biomass for bioenergy**

Renewable energy is currently estimated to provide only 15% of the global primary energy supply [8], despite increasing concern about rises in atmospheric carbon arising from fossil fuel combustion. Recent environmental commitments by major countries, including the UK and USA, have focussed attention on the
potential of renewable bioenergy as a means of alleviating dependence on depleting fossil fuel reserves and reducing CO₂ emissions. However, production of biomass for energy, in particular that derived from annual crops, such as maize and wheat, has been a source of much debate [74-75]. Annual crops, (crops grown for one growing season), currently contribute significantly to the global bioenergy market, but yields are dependent on high nutrient inputs. In contrast, perennial grasses and tree crops, (crops with a life span of more than 2 yr) can achieve higher biomass yields with relatively lower inputs of nitrogen fertilizer [78]. For example, SRC plantations throughout Europe were capable of yielding high amounts of biomass without need for fertilisers [79], suggesting that it is possible in many cases to balance ecological and economic objectives by proper soil management. The proportion of global energy diverted to nitrogen fertiliser production and use is estimated at 2%, so fertiliser applications greatly affect the overall energy cost and balance within a system.

Woody biomass crop production has largely been driven by the ability of fast-growing members of the Salicaceae, such as *Populus* (poplar) and *Salix* (willow), and other genera such as *Eucalyptus* and *Acacia* to regenerate vegetatively following coppicing, with coppices typically occurring every 4-16 years, although longer coppice cycles (up to 30 yr) are also practiced [3]. Characteristically, many poplar and willow species meet the criteria as suitable species for energy harvest, including fast growth, high yield and the ability to grow on marginal land. In addition, biomass plantation management could benefit from the genotypic variability associated with members of the Salicaceae, whereby desirable attributes, such as pest and disease resistance, are identified and exploited to enhance biomass production. Practice of ‘naturalistic’ SRC forestry [3],
whereby tree species are selected based on their suitability for a particular site, could have positive effects on biomass production on marginal or waste land. Manipulating plant species with broad genetic variability to produce favourable hybrids, plus establishing suitable combinations of plant, mycorrhizal and bacterial species [70], could maximise plant growth benefits in SRC forestry. Future studies should attempt to elucidate the complex interactions among the relevant mycorrhizal fungi, soil microbes and commercial varieties of SRC crops in the field.

Box 2. Carbon sequestration in SRC forestry

Mitigation of global climate change can be partially achieved by increasing the carbon sink of terrestrial ecosystems, most importantly through changes in land use and management [15]. It is generally accepted that the potential for soil carbon sequestration is enhanced under conditions of minimal disturbance, high soil biomass, improved soil structure, conservative nutrient cycling, and high faunal and microbial biodiversity. These factors intrinsically link soil carbon storage to non-intensive land management, such as sustainably managed SRC plantations. Incidentally, relatively undisturbed forests generally also have higher mycorrhizal biomass (e.g. up to 30% of the microbial biomass was accounted for by ECMF in a boreal forest soil [34]), which represents a significant terrestrial sink for photosynthetically fixed carbon. Evidence for long-term carbon storage under SRC plantations remains scarce, however, although it has been simulated that SRC forests divert more carbon belowground than do regenerated woodlands [4]. In a study of natural $^{13}$C abundance in vertical soil gradients of a 68-yr-old Norway spruce forest, older microbially derived carbon was identified as the main contributor to soil respiration at soil depths below 20 cm [80]. This suggests that
microbial immobilisation of carbon is important in soil carbon cycling in forests.

Evidence of the impacts of SRC on soil carbon sequestration is lacking mainly owing to problems surrounding the evaluation of slow processes such as carbon sequestration on relatively recently established SRC plantations (since the 1980’s) [4]. Research into carbon sequestration under SRC willow and poplar in the US indicated that an initial loss of soil carbon occurred during the first years after plantation establishment, possibly due to enhanced decomposition. Over the 18-year study, however, carbon was sequestered at an average rate of 1.6 Mg ha\(^{-1}\) yr\(^{-1}\) compared with control fields, which was attributed to increases in leaf litter inputs and slower rates of decomposition [4]. Effectively, biomass could be used to remove surplus CO\(_2\) from the atmosphere and, particularly when combined with biochar production, offer a source of carbon neutral energy. Nitrogen addition to forests has also been implicated in increased soil carbon sequestration [81] although at present there is much debate on this topic, particularly with regards to possible increases in greenhouse gases emissions, such as methane and nitrous oxide [82]. Although development of strategies to increase future soil carbon storage will require further study, land management strategies that incorporate the use of biochar (see Glossary), such as sustainable SRC plantations, could have particular significance for soil carbon sequestration in the long term.

Glossary

**Arbuscular mycorrhizal fungi (AMF):** members of the monophyletic group, Glomeromycota, characterised by formation of distinct intracellular ‘arbuscules’ within the root system.
Biochar: a derivative of biomass carbon, formed when biomass is partially combusted in the absence of oxygen.

Bioenergy: energy that is sourced from biologically derived matter, including combustible woodfuel, wood waste, crop residues, municipal waste and ethanol production from cereals and other crops.

Biomass energy: carbon-based renewable energy derived from plant matter.

Carbon-neutral energy: energy consumption whereby the carbon released does not increase current atmospheric carbon levels.

Cropping security: the protection of economically valuable crops and yields from the effects of potential stresses including extreme climate events, pests, diseases and invasive species.

Ectomycorrhizal fungi (ECMF): characterised by hyphal growth between root cortical cells, known as the Hartig net, often with a fungal sheath (mantle) enclosing root tips.

Extraradical mycelia: external (outside root) phase of mycorrhizal fungi, formed by both AMF and ECMF hyphae, extending the area over which nutrients can be taken up or released.

Functional complementarity: (in mycorrhizas) performance of different functions by mycorrhizal fungal species, which confer contrasting benefits on the associated plant.

Mycorrhizal hyphosphere: volume of soil influenced biologically, chemically or physically by mycorrhizal fungal hyphae.

Mycorrhizas: literally ‘fungus-root’, a symbiotic association between plants and soil fungi.
Mycorrhizosphere: volume of soil influenced biologically, chemically or physically by both growing plant roots (often colonised by mycorrhizas) and mycorrhizal fungal hyphae.

Plant-growth promoting rhizobacteria (PGPR): soil bacteria that positively affect plant growth and/or nutrition, either directly or indirectly.

Rhizodeposition: carbon release to soil via plant roots (including the mycorrhizal component), which includes passive exudation of low molecular weight compounds, active secretion of high molecular weight compounds, lysates released from dead root cells, mucilages and dead roots.

Rhizosphere: volume of soil influenced biologically, chemically or physically by the growing plant root.

Short rotation coppice (SRC): forestry practice of removing aboveground plant biomass only, allowing vegetative regeneration of the next crop. Coppicing typically occurs every 3-5 years.

**Figure 1.** *Populus* (poplar) roots with ectomycorrhizal and arbuscular mycorrhizal structures. (a) fine poplar root tips are covered with an ectomycorrhizal sheath (s) with thread-like hyphae extending from the root creating a mycelial network (m). An outer sheath-like structure or fungal mantle often encloses fine root tips that have been colonised by ectomycorrhizal fungi; (b) intracellular arbuscule (arb) invaginating a poplar root cell. Arbuscules are a characteristic feature of arbuscular mycorrhizas and nutrient exchange probably occurs here. Scale bars: (a) 0.3mm (b) 10 µm
Figure 2. Potential effects of mycorrhizas on biomass crop functions and performance (yield and cropping security). Photo: Short rotation coppice plantation on agricultural land near Uppsala, central Sweden (M. Weih)