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1 **Mycorrhizas and biomass crops: opportunities for future sustainable**

2 **development**

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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 CO_2 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

51 agricultural sustainability, by enhancing regulation of important ecological

52 processes [1]. Although willow SRC is commercially grown in several countries

53 including Sweden (~14000 ha), the production of biomass for energy from SRC

54 forestry is still in the experimental stages of development in major countries such

55 as the UK and US [2]. Land availability and biomass yield are major concerns

56 surrounding biomass as an energy source [3-7], yet the contribution of biomass

57 derived energy to global renewable energy stocks (~50% in 2004) remains

58 significant [8].

59   Less attention, however, has focussed on sustainable SRC culture,

60 including interactions with soil microbial communities. As primary producers, plants

61 provide photosynthetically derived carbon to the soil microbial community,

62 including symbiotic mutualists, decomposers and pathogens [9] via rhizodeposition

63 [10] which is easily assimilated by the soil microbial biomass [11,12]. A vital

64 component of the soil microbial community, mycorrhizal fungi, represent the

65 primary interface between photosynthate and soil through intimate associations

66 with plant roots, and have a central role in plant nutrient acquisition and plant

67 health [13]. Interestingly, the perennial nature of SRC crops is associated with

68 minimal mechanical disturbance of soil and is likely to promote belowground

69 mycorrhizal functioning which, in turn, could promote biomass yield and cropping

70 security. Compared with conventional cropping systems, SRC plantations are only

71 replanted every 10-25 years (depending on national regulation, market issues and

72 plantation health), which significantly lengthens crop-rotation periods and the crop

73 is generally more deeply-rooted, requiring no annual soil cultivation or herbicide

74 application once established (Box 1). In addition, considerably less agrochemical

75 inputs, in particular nitrogen, are required in SRC. Non-intensive management of

76 SRC plantations may also present significant potential for belowground carbon

77 sequestration [14,15], which can improve soil quality in SRC (Box 2). Carbon

78 sequestration is especially relevant to renewable energy production as it

79 represents an additional carbon offset compared with fossil fuel emissions.

80 Understanding plant-microbial interactions is crucial to our understanding of

81 soil ecosystem function and its role in sustainable land management. Here we

82 discuss the potential importance of interactions between mycorrhizas and biomass

83 crops in SRC systems, with particular reference to the sustainable generation of

84 biomass for renewable energy and the potential for carbon sequestration.

85

86 **Mycorrhizas in biomass crop plantations**

87 Mycorrhizal fungi are an important integral component of the plant-soil

88 system, forming symbiotic associations with most land plants and mediating a

89 range of crucial ecosystem processes [13,16]. In return for photosynthetically

90 derived carbon, mycorrhizal fungi have a fundamental role in plant nutrition, most

91 notably in the provision of phosphorus and nitrogen to the host plant [13]. In

92 addition, other non-nutritional benefits, such as soil aggregation and stability [17],

93 increased drought tolerance, and protection against pathogens [18, 19] can be

94 conferred upon the associated host. Although mycorrhizas have been found

95 associated with several biomass-producing plant species, such as *Populus* and

96 *Salix* species [20-25], information concerning their functional role in SRC

97 plantations is scarce.

98 Two major types of mycorrhizal fungi, the arbuscular mycorrhizal fungi

99 (AMF) and the ectomycorrhizal fungi (ECMF), form symbiotic associations with

100 most land plants. AMF (~200 species described) are likely to have coevolved with

101 terrestrial plants, at least partially facilitating the colonisation of land by plants over

102 400 million years ago [26] and can form associations with approximately two-thirds

103 of land plants. ECMF (~6000 species described) are likely to have evolved later

104 (130 million years ago) and are generally associated with woody plants [13]. Both

105 AMF and ECMF support extensive extraradical hyphal networks maintained by

106 plant-fixed carbon (Figure 1), which act as a conduit for nutrient exchange between

107 plant roots and the soil environment. Interestingly, the main tree genera used in

108 biomass plantations worldwide *(Salix, Populus* and *Eucalyptus)* can form both AMF

109 and ECMF associations, occasionally with AMF and ECMF present in the same

110 root system [27]. Such 'dual-colonisation' can result from several factors, including

111 successional stages in tree development (as the tree matures and the root

112 develops) [28], availability of mycorrhizal inoculum strength (availability of fungal

113 spores and/or hyphal fragments) [25], local soil conditions [13] or geographical

114 location [29]. It is possible that different mycorrhizal types or species associated

115 with a given plant could offer functional complementarity (see Glossary) [30].

116 However, although dually-colonised trees in SRC plantations have been reported

117 [23,25,27,31], it is usually one type of mycorrhizal association that dominates or

118 exclusively colonises a given plant at any one time. Studies of willow plantations

119 revealed ECMF as the dominant mycorrhizal association, with AMF accounting for

120 significantly lower root colonisation, often <1% [20,23-25,31]. Similarly, ECMF,

121 rather than AMF, dominated both willow and poplar stands on afforested sites in

122 Northern Germany [32].

123   Growth and maintenance of mycorrhizal structures is supported by plant-

124 fixed carbon, and establishment of mycorrhizal symbioses therefore comes at a

125 carbon 'cost' to the plant. Extraradical (outside the root) hyphal growth is often

5

126 extensive and can account for up to 30% of the microbial biomass in soil [33,34].

127 Plant investment in mycorrhizas is offset by the benefits gained (such as increased

128 nutrient acquisition) in most cases, hence mycorrhizal associations are considered

129 mutualistic. In fact, plant investment in mycorrhizal hyphae 'cost' the plant 100

130 times less carbon to construct a unit of hypha than it would that of a root [35],

131 effectively making the symbiosis cost-effective in terms of plant carbon investment,

132 especially as hyphae can extend beyond the nutrient depletion zone that develops

133 around the roots. Plant investment in mycorrhizas should therefore decline as soil

134 nutrient availability increases, as an abundance of labile nutrients (such as fertiliser

135 additions) reduces the need for a foraging symbiont. However, the sparse

136 experimental evidence for nutrient fertilization effects on mycorrhizal colonization

137 of SRC crops indicates variable relationships: fertilization either reduced or

138 increased mycorrhizal colonisation of SRC willow, depending on soil and/or other

139 site-specific conditions [20]. Increased understanding about the relationships

140 between soil nutrient availability and mycorrhizal colonisation in SRC could be

141 used to develop marginal land for SRC forestry, thus reducing competition for high-

142 quality agricultural land, which is increasingly in demand to fulfil global food and

143 housing requirements [36].

144

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

146 A main feature of mycorrhizal symbioses is carbon flux from the plant to the

147 fungal symbiont, making mycorrhizas an integral link in global carbon cycling.

148 Mycorrhizal colonisation alters the carbon metabolism of the plant, increasing the

149 carbon allocation to the whole root system [37], with a significant proportion (4-

150 20%) diverted to the fungal component [12,38,39]. $^{13}CO_2$ labelling experiments

151 have indicated that carbon translocation to fungal hyphae can be rapid (within 24

152 hr of fixation; [38]), although slower delivery rates of up to 4 days post-labelling

153 have also been reported [40]. Poplar and willow species support substantial root

154 systems, presumably with a significant proportion of fixed carbon allocated to the

155 roots, which can be stored in the root system to support new shoot development

156 following a coppicing cycle [41]. It is currently unknown how mycorrhizal carbon

157 flux is altered during coppicing cycles, especially with regards to carbon allocation

158 to the fungal component when the aboveground biomass is harvested. It is

159 possible that coppicing causes the plant to initially retain its carbon store for self-

160 regeneration, until there is 'need' to divert some to the fungal component (i.e. when

161 mineral nutrients become limiting for growth).

162   Characteristic mycorrhizal exudates including amino acids, organic acids,

163 sugars and polysaccharides have been identified [42-45] and can be quickly

164 assimilated by the soil microbial biomass. Additionally, other fungal-specific

165 exudates, such as glomalin (a fungal glycoprotein), are produced by AMF.

166 Glomalin is highly persistent in soil (residence time of 4-62 yr) and acts as soil

167 'glue', which can improve soil structure by enhanced soil aggregation [46,47].

168 Qualitative and quantitative differences in mycorrhizal exudates might also

169 contribute to soil chemical, physical and biological heterogeneity, creating hotspots

170 of microbial activity and promoting soil activity. However, incorporation of recently

171 fixed carbon into the soil microbial biomass represents only one route for the total

172 diverted carbon, with a substantial carbon diversion to other fungal structures,

173 particularly investment in the external mycelial network. Carbon turnover from fine

174 AMF hyphae can be rapid (5-6 days) with thicker hyphae taking up to 30 days [48],

175 thus representing an important pathway by which plant-assimilated carbon enters

176 the soil environment [49]. This is in contrast to root turnover, which can take

177 several years depending on the root diameter and plant species [50]. Difficulties

178 arise in attempting to apply these turnover times to all fungal tissues, however,

179 especially if considering the carbon investment associated with the extraradical

180 mycelial network or characteristic fungal structures. Intraradical vesicles,

181 reproductive spores, arbuscules (in AMF), intra- and extraradical hyphae

182 collectively consume a large fraction of carbon allocated to the fungus. This carbon

183 pool is likely to have a much longer mean residence time in soil [51] than 5-6 days;

184 an observation which is supported by data suggesting that the residence time of

185 carbon in ECMF communities is 4-5 years [52]. Collectively, these data suggest

186 that mycorrhizas contribute to short and long-term soil organic carbon pools [47,

187 51].

188   In terms of carbon sequestration, long-term belowground storage of plant-

189 fixed carbon in stable organic forms derived from fungal spores and glomalin (the

190 latter by AMF only) offers a means of carbon storage in a relatively stable form.

191 Soil organic matter accumulation was shown to significantly increase in both willow

192 and poplar biomass plantations in the six years following afforestation of arable

193 sites, which was attributed to inputs from leaf and root litter from the newly

194 established stands [32]. Additionally, this increase in organic matter content was

195 implicated in the increased ECMF associations in the same willow and poplar

196 plantations [32]. An interesting concept arising from biomass production is that of

197 biochar generation. Biochar is a derivative of biomass carbon, formed when

198 biomass is partially combusted (in the absence of oxygen) to generate energy.

199 Such partial combustion typically releases ~50% of the carbon contained in the

200 biomass and produces a carbon-rich powdery substance (biochar) as an end

201 product, which can be added back to the soil for long term storage. Biochar has the

202 potential to sequester up to 40% of initial biomass carbon owing to its long

203 residence time in soil (thousands of years) compared with complete combustion,

204 which retains ~3% carbon, and decomposition, which can sequester only up to

205 20% carbon after ten years [53]. Biochar addition to soil can also have positive

206 effects on mycorrhizal status, notably with increases in root colonisation [54]. The

207 effects of biochar on mycorrhizas can be attributed to changes in soil physico-

208 chemical factors, such as nutrient availability and microbial activity. The exact

209 mechanisms governing mycorrhizal responses to biochar in soil require further

210 investigation however, particularly with regards to ERM dynamics. Quantification of

211 the contributions of biochar to soil carbon storage in SRC systems is also an

212 important consideration for future energy production from biomass (Box 2).

213

214 SRC, nutrient cycling and mycorrhizas

215 Coppicing is practiced in forestry as a means of removing apical dominance

216 to encourage accelerated growth and increased yields, and in SRC plantations

217 coppicing typically occurs every 3-5 years [41]. Following coppicing, re-growth of

218 new plant biomass is facilitated by the regeneration of new shoots from the

219 remaining stump. Conventional land management practices often include tillage

220 and significant inputs of nutrients, herbicides and pesticides can have negative

221 impacts on the number of mycorrhizal species present and can, in effect,

222 marginalise mycorrhizal and microbial functioning [19,55,56]. In commercial SRC

223 culture, the use of herbicides is required only during establishment of the plantation

224 and pesticide application is generally not required [57]. SRC plantations could

225 therefore be managed organically after the establishment phase, as a total

226 absence of fertilisation could allow biomass yield to decline to economically

227 unfeasible levels. Extrapolating these data to SRC biomass plantations is difficult

228 however, as interactions with other site-specific variables can alter mycorrhizal

229 dynamics in soil.

230   Preservation of soil microbiology in less intensively managed sites can

231 contribute to self-regulation of fundamental ecosystem processes, particularly

232 nutrient recycling, without need for further nutrient inputs. Given the support for

233 mycorrhizal enhancement of plant nutrient status [13], however, the problem of

234 nutrient limitation of yield can be alleviated by mycorrhizal retrieval of nitrogen and

235 phosphorus from soil organic material. High-yielding perennial trees, such as those

236 grown in biomass plantations, can generally produce high dry matter yields from

237 modest nitrogen applications (20-50% less nitrogen fertilisation than annual crops)

238 [41]. This may mean that nitrogen inputs to SRC plantations can often be kept to a

239 minimum (at least compared to many conventional agricultural practices), thereby

240 minimising the possibility of adverse environmental impacts which may ensue if

241 excess nitrogen is applied to the land. Closure of major nutrients cycles, such as

242 nitrogen cycling, is one of the most important factors in ecologically sustainable

243 systems, as it lowers the amount of nitrogen leached out or lost in gaseous form.

244   Enhancing the availability of phosphorus and nitrogen to host plants is

245 considered the most important function of mycorrhizas [13], and nutrient availability

246 in sustainable systems is often dependent on mycorrhizal activity. Phosphorus is a

247 major nutrient required by plants, although in soil it is usually present in very low

248 concentrations [13], as soluble phosphorus is readily taken up by both plants and

249 microbes. Investment in mycorrhizas therefore means that plants can indirectly

250 access nutrients beyond the nutrient depletion zone of the roots via extensive

251   mycelial networks. Both AMF and ECMF can effectively forage for relatively

252   insoluble forms of soil inorganic phosphorus, such as rock phosphate, iron

253   phosphates and aluminium phosphates [13]. In addition, ECMF have a major role

254   in recycling soil organic nitrogen and organic phosphorus which are unavailable to

255   the plant. In some forests, ECMF can suppress the activity of saprotrophs, a

256   process known as 'the Gadgil effect', whereby ECMF inhibition of saprotrophic

257   microbes was implicated in reduced litter decomposition, allowing accumulation of

258   organic matter in the soil [58]. This could have been due to ECMF being supplied

259   with energy from their plant host, which could give them a competitive advantage

260   over saprotrophs. Although it is not clear how these processes are regulated in

261   SRC forests, these actions suggest a possible niche role for efficient nutrient

262   cycling under low-input systems. By contrast, the role of AMF in retrieval of organic

263   nitrogen is unclear as AMF are not known to have any saprotrophic capabilities,

264   although AMF involvement in nitrogen capture from complex organic sources has

265   previously been demonstrated in laboratory conditions [59,60].

266

267   **Effects of mycorrhizas on soil biodiversity**

268   Mycorrhizal persistence under sustainably managed SRC could promote

269   soil biological diversity through further symbiotic interactions with important soil

270   organisms. For example, specific bacterial groups often associate with mycorrhizal

271   hyphae [61], including plant growth-promoting rhizobacteria (PGPR) [62,63] which

272   are important contributors to overall plant growth and/or nutrition. In addition, some

273   bacterial communities were shown to specifically attach to dead AMF hyphae,

274   whereas others used exudates from living hyphae as a growth substrate, the latter

275   including two known PGPRs (*Pseudomonas fluorescens* SBW25 and *Paenibacillus*

276   *brailensis* PB177) [64]. Mycorrhiza helper bacteria (MHB) have been identified as

277   important components of both AMF and ECMF hyphospheres and are capable of

278   increasing rates of mycorrhizal colonisation and suppressing soil pathogens [65]. A

279   recent study demonstrated the effectiveness of introducing both selected

280   mycorrhizal fungal and bacterial species to poplar seedlings at the nursery stage,

281   where co-inoculation increased plant nutrient status and increased establishment

282   success at various sites [66]. Furthermore, interactions with higher trophic

283   organisms are enhanced by mycorrhizal presence, in particular hyphal predators

284   such as collembolans, nematodes and mites [67,68], although little is currently

285   known about the underlying mechanisms that govern these interactions. Hyphal

286   grazing emphasises a further positive impact that mycorrhizas can have on soil

287   food webs and soil biodiversity, the consequences of which might mean greater

288   ecosystem productivity [69] and greater soil carbon storage. Difficulties are faced

289   when attempting to extrapolate this sparse knowledge, derived mainly from

290   microcosm work, to the field and specifically to SRC biomass plantations.

291   Another interesting example regarding the effects of mycorrhizas on higher

292   trophic organisms is represented by the interactions between root mycorrhizal

293   colonization and leaf herbivore resistance in willows [70]. In fact, mycorrhizas and

294   their influence on crop resistance to phytophagous insects might involve a yet

295   unexplored potential for the bioprotection of agricultural crops. Control of pests and

296   diseases in biomass plantations is important for the maintenance of high yields (i.e.

297   crop security). Plant resistance to insect attack is often mediated by tissue

298   concentrations of phenolic compounds that affect insect behaviour, development

299   and survival. In an experimental study, the effects of mycorrhizas on willow leaf

300   chemistry were found to be dependent on specific combinations of fungal species

301 and plant genotype [70]. Mycorrhizal control over the production of plant foliar

302 substances (e.g. salicylic acid) could therefore present opportunities for selection

303 of compatible fungal and plant combinations to combat herbivory. In effect, this

304 presents a conceptual basis for the development of biological control strategies

305 against insect herbivory in willow and poplar biomass plantations.

306

307 **Challenges for future research**

308 The theoretical potential of bioenergy is vast, and considerable emphasis

309 must be placed on conducting large-scale field trials to optimise biogeochemical

310 conditions for sustainable biomass production. Many groups of organisms regulate

311 essential ecosystem processes, but mycorrhizal fungi arguably represent the most

312 important keystone group linking crop productivity and cropping security to below

313 ground functioning (Figure 2). The preservation of mycorrhizal status in biomass

314 plantations could significantly improve the viability of low-input SRC plantations.

315 However, lack of information regarding the underlying functional relationships

316 between plants, mycorrhizas, pests and microorganisms represents a major

317 challenge in the attempt to achieve sustainability. We have identified the following

318 areas which merit further investigation: the effects of mycorrhizas on biomass

319 production and carbon sequestration under various management regimes; the

320 effects of nutrient fertilization, regular harvests and biochar application on

321 mycorrhizal functioning; the interactions between mycorrhizal fungal genotype and

322 crop genotype. Another prerequisite for the successful implementation of

323 sustainable management concepts into SRC culture is the consideration of

324 ecological processes in crop breeding, as specific fungal – host genotype

325 combinations seem to be crucial for the ultimate effects of mycorrhizas on crop

326 performance and pest resistance [70,71]. Resolution of such issues will contribute

327 greatly to our understanding of how sustainable land management and future

328 energy needs may be achieved.

329 Depletion of finite resources, such as global phosphate reserves, which are

330 estimated to run out ~100-150 years from now, based on current exploitation rates

331 [77, 78] suggests that management of organisms, such as mycorrhizal fungi, which

332 can exploit and recycle soil phosphorus and nitrogen is advantageous. Integration

333 of mycorrhizal systems with other carbon sequestration management practices, for

334 example biochar usage [53,54] (Box 2), could also be an important future practice.

335 The first mycorrhizal symbioses evolved over 400 million years ago in response to

336 phosphorus deficiency in terrestrial ecosystems [35], and we suggest that

337 capitalisation on this strategy in sustainably managed ecosystems could become

338 essential for future land management and crop production.

339

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535

536 **Box 1. Biomass for bioenergy**

537 Renewable energy is currently estimated to provide only 15% of the global

538 primary energy supply [8], despite increasing concern about rises in atmospheric

539 carbon arising from fossil fuel combustion. Recent environmental commitments by

540 major countries, including the UK and USA, have focussed attention on the

541   potential of renewable bioenergy as a means of alleviating dependence on

542   depleting fossil fuel reserves and reducing CO_2 emissions. However, production of

543   biomass for energy, in particular that derived from annual crops, such as maize

544   and wheat, has been a source of much debate [74-75]. Annual crops, (crops grown

545   for one growing season), currently contribute significantly to the global bioenergy

546   market, but yields are dependent on high nutrient inputs. In contrast, perennial

547   grasses and tree crops, (crops with a life span of more than 2 yr) can achieve

548   higher biomass yields with relatively lower inputs of nitrogen fertilizer [78]. For

549   example, SRC plantations throughout Europe were capable of yielding high

550   amounts of biomass without need for fertilisers [79], suggesting that it is possible in

551   many cases to balance ecological and economic objectives by proper soil

552   management. The proportion of global energy diverted to nitrogen fertiliser

553   production and use is estimated at 2%, so fertiliser applications greatly affect the

554   overall energy cost and balance within a system.

555   Woody biomass crop production has largely been driven by the ability of

556   fast-growing members of the Salicaceae, such as *Populus* (poplar) and *Salix*

557   (willow), and other genera such as *Eucalyptus* and *Acacia* to regenerate

558   vegetatively following coppicing, with coppices typically occurring every 4-16 years,

559   although longer coppice cycles (up to 30 yr) are also practiced [3].

560   Characteristically, many poplar and willow species meet the criteria as suitable

561   species for energy harvest, including fast growth, high yield and the ability to grow

562   on marginal land. In addition, biomass plantation management could benefit from

563   the genotypic variability associated with members of the Salicaceae, whereby

564   desirable attributes, such as pest and disease resistance, are identified and

565   exploited to enhance biomass production. Practice of 'naturalistic' SRC forestry [3],

566   whereby tree species are selected based on their suitability for a particular site,

567   could have positive effects on biomass production on marginal or waste land.

568   Manipulating plant species with broad genetic variability to produce favourable

569   hybrids, plus establishing suitable combinations of plant, mycorrhizal and bacterial

570   species [70], could maximise plant growth benefits in SRC forestry. Future studies

571   should attempt to elucidate the complex interactions among the relevant

572   mycorrhizal fungi, soil microbes and commercial varieties of SRC crops in the field.

573

574   **Box 2. Carbon sequestration in SRC forestry**

575   Mitigation of global climate change can be partially achieved by increasing

576   the carbon sink of terrestrial ecosystems, most importantly through changes in land

577   use and management [15]. It is generally accepted that the potential for soil carbon

578   sequestration is enhanced under conditions of minimal disturbance, high soil

579   biomass, improved soil structure, conservative nutrient cycling, and high faunal

580   and microbial biodiversity. These factors intrinsically link soil carbon storage to

581   non-intensive land management, such as sustainably managed SRC plantations.

582   Incidentally, relatively undisturbed forests generally also have higher mycorrhizal

583   biomass (e.g. up to 30% of the microbial biomass was accounted for by ECMF in a

584   boreal forest soil [34]), which represents a significant terrestrial sink for

585   photosynthetically fixed carbon. Evidence for long-term carbon storage under SRC

586   plantations remains scarce, however, although it has been simulated that SRC

587   forests divert more carbon belowground than do regenerated woodlands [4]. In a

588   study of natural ^{13}C abundance in vertical soil gradients of a 68-yr-old Norway

589   spruce forest, older microbially derived carbon was identified as the main

590   contributor to soil respiration at soil depths below 20 cm [80]. This suggests that

591 microbial immobilisation of carbon is important in soil carbon cycling in forests.

592 Evidence of the impacts of SRC on soil carbon sequestration is lacking mainly

593 owing to problems surrounding the evaluation of slow processes such as carbon

594 sequestration on relatively recently established SRC plantations (since the 1980's)

595 [4]. Research into carbon sequestration under SRC willow and poplar in the US

596 indicated that an initial loss of soil carbon occurred during the first years after

597 plantation establishment, possibly due to enhanced decomposition. Over the 18-

598 year study, however, carbon was sequestered at an average rate of 1.6 Mg ha^{-1}yr^{-1}

599 compared with control fields, which was attributed to increases in leaf litter inputs

600 and slower rates of decomposition [4]. Effectively, biomass could be used to

601 remove surplus CO_2 from the atmosphere and, particularly when combined with

602 biochar production, offer a source of carbon neutral energy. Nitrogen addition to

603 forests has also been implicated in increased soil carbon sequestration [81]

604 although at present there is much debate on this topic, particularly with regards to

605 possible increases in greenhouse gases emissions, such as methane and nitrous

606 oxide [82]. Although development of strategies to increase future soil carbon

607 storage will require further study, land management strategies that incorporate the

608 use of biochar (see Glossary), such as sustainable SRC plantations, could have

609 particular significance for soil carbon sequestration in the long term.

610

611 **Glossary**

612 **Arbuscular mycorrhizal fungi (AMF):** members of the monophyletic group,

613 Glomeromycota, characterised by formation of distinct intracellular 'arbuscules'

614 within the root system.

615 **Biochar:** a derivative of biomass carbon, formed when biomass is partially

616 combusted in the absence of oxygen.

617 **Bioenergy:** energy that is sourced from biologically derived matter, including

618 combustible woodfuel, wood waste, crop residues, municipal waste and ethanol

619 production from cereals and other crops.

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

621 **Carbon-neutral energy:** energy consumption whereby the carbon released does

622 not increase current atmospheric carbon levels.

623 **Cropping security:** the protection of economically valuable crops and yields from

624 the effects of potential stresses including extreme climate events, pests, diseases

625 and invasive species.

626 **Ectomycorrhizal fungi (ECMF):** characterised by hyphal growth between root

627 cortical cells, known as the Hartig net, often with a fungal sheath (mantle)

628 enclosing root tips.

629 **Extraradical mycelia:** external (outside root) phase of mycorrhizal fungi, formed

630 by both AMF and ECMF hyphae, extending the area over which nutrients can be

631 taken up or released.

632 **Functional complementarity:** (in mycorrhizas) performance of different functions

633 by mycorrhizal fungal species, which confer contrasting benefits on the associated

634 plant.

635 **Mycorrhizal hyphosphere:** volume of soil influenced biologically, chemically or

636 physically by mycorrhizal fungal hyphae.

637 **Mycorrhizas:** literally 'fungus-root', a symbiotic association between plants and

638 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

662 **Figure 2.** Potential effects of mycorrhizas on biomass crop functions and

663 performance (yield and cropping security). Photo: Short rotation coppice plantation

664 on agricultural land near Uppsala, central Sweden (M. Weih)