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Authors:	Deirdre C. Rooney, Ken Killham, Gary D. Bending, Elizabeth Baggs, Martin Weih and Angela Hodge
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1 **Mycorrhizas and biomass crops: opportunities for future sustainable**  
2 **development**

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5 Deirdre C. Rooney<sup>1</sup>, Ken Killham<sup>2</sup>, Gary D. Bending<sup>3</sup>, Elizabeth Baggs<sup>2</sup>, Martin  
6 Weih<sup>4</sup> and Angela Hodge<sup>1</sup>

7

8 <sup>1</sup>Department of Biology, University of York, Area 14, PO Box 373, York, YO10  
9 5YW, UK

10 <sup>2</sup>Institute of Biological and Environmental Sciences, Cruickshank Building, St.  
11 Machar Drive, Aberdeen, AB24 3UU, UK

12 <sup>3</sup>Warwick HRI, University of Warwick, Wellesbourne, Warwick, CV35 9EF, UK

13 <sup>4</sup>Department of Crop Production Ecology, Box 7043, 750 07, Uppsala, Sweden

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

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26 **Abstract**

27 Central to soil health and plant productivity in natural ecosystems are *in situ*  
28 soil microbial communities, of which mycorrhizal fungi are an integral component,  
29 regulating nutrient transfer between plants and the surrounding soil via extensive  
30 mycelial networks. Such networks are supported by plant-derived carbon and are  
31 likely to be enhanced under coppiced biomass plantations, a forestry practise that  
32 has been highlighted recently as a viable means of providing an alternative source  
33 of energy to fossil fuels, with potentially favourable consequences for carbon  
34 mitigation. Here, we explore ways in which biomass forestry, in conjunction with  
35 mycorrhizal fungi, can offer a more holistic approach to addressing several topical  
36 environmental issues, including 'carbon-neutral' energy, ecologically sustainable  
37 land management and CO<sub>2</sub> sequestration.

38

39 **Sustainable biomass production for future energy needs**

40 Current developments in agriculture have involved growing bioenergy crops  
41 on agricultural land, with a shift in focus from yield- and quality-related issues  
42 towards more sustainable forms of agriculture [1]. A major challenge facing global  
43 bioenergy production is striking the balance between long-term sustainability, and  
44 reaching short-term productivity goals if bioenergy is to become a viable means of  
45 reducing fossil fuel dependency. 'Sustainability' in agriculture is difficult to define  
46 unequivocally, but often involves minimal chemical inputs, efficient nutrient  
47 recycling and enhancement of important microbial-driven processes such as  
48 nutrient acquisition, decomposition and protection against pathogens. Perennial  
49 crops, such as *Salix* (willow) and *Populus* (poplar) species, grown in short rotation  
50 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

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]. <sup>13</sup>CO<sub>2</sub> 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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343

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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<sub>2</sub> 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  $^{13}\text{C}$  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  $1.6 \text{ Mg ha}^{-1}\text{yr}^{-1}$   
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  $\text{CO}_2$  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.

639 **Mycorrhizosphere:** volume of soil influenced biologically, chemically or physically  
640 by both growing plant roots (often colonised by mycorrhizas) and mycorrhizal  
641 fungal hyphae.

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

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

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

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

653

654 **Figure 1.** *Populus* (poplar) roots with ectomycorrhizal and arbuscular mycorrhizal  
655 structures. (a) fine poplar root tips are covered with an ectomycorrhizal sheath (s)  
656 with thread-like hyphae extending from the root creating a mycelial network (m). An  
657 outer sheath-like structure or fungal mantle often encloses fine root tips that have  
658 been colonised by ectomycorrhizal fungi; (b) intracellular arbuscule (arb)  
659 invaginating a poplar root cell. Arbuscules are a characteristic feature of arbuscular  
660 mycorrhizas and nutrient exchange probably occurs here. Scale bars: (a) 0.3mm  
661 (b) 10  $\mu\text{m}$

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)