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25 **Abstract**

26 Microbial solar cells (MSCs) are recently developed technologies utilizing solar energy to
27 produce electricity or chemicals. MSCs use photoautotrophic microorganisms or higher
28 plants to harvest solar energy, and use electrochemically active microorganisms in the
29 bioelectrochemical system to generate electrical current. Here, we review the principles and
30 performance of various MSCs, in an effort to identify the most promising systems as well as
31 the bottlenecks and potential solutions towards ‘real life’ MSC application. We give an
32 outlook on future applications based on the intrinsic advantages of MSCs, showcasing
33 specifically how these living energy systems can facilitate the development of an electricity-
34 producing green roof.

35

36 **Background**

37 Society is facing local and global challenges to secure the needs of people and planet ^[1, 2].
38 One of those needs is energy, which should be available in the form of electricity or fuels,
39 ideally produced from a renewable source via an efficient and clean conversion process. The
40 microbial solar cell (MSC) is a new collective name of biotechnological systems that
41 integrate photosynthetic and electrochemically active organisms to generate *in situ* “green”
42 electricity or chemical compounds, such as hydrogen, methane, ethanol and hydrogen
43 peroxide ^[3-5]. MSC is a recent development that builds on the discovery of electrochemically
44 active bacteria and subsequent development of microbial fuel cells (MFCs) ^[6-10]. The MFC
45 typically cleans wastewater and generates electricity from organic compounds present.
46 Within the MFC, electrochemically active bacteria at the anode oxidize organic compounds
47 and deliver electrons to the anode. These electrons flow through a power harvester to the
48 cathode, where electrons are delivered to reduce oxygen ^[11]. In a MSC, the photosynthetic
49 organisms use sunlight to produce organic matter that is further converted into electricity
50 using the MFC ^[9, 12, 13]. The most investigated MSC is the plant microbial fuel cell (PMFC),
51 which has a living plant that delivers organic matter via its roots to electrochemically active
52 bacteria in the MFC ^[12, 14-19].

53 Our aim is to review the principles and performance of MSCs, presenting the
54 challenges and the outlook for future applications of these technologies. Various MSCs have
55 been recently described, which can be categorized according to the way solar energy is
56 captured and the mode of organic matter transfer from the photosynthetic portion to the fuel
57 cell. Both reported and potential performance of the different MSCs are analyzed to
58 recognize bottlenecks and to identify solutions. Currently, it is not possible to predict the
59 cost-effectiveness of the technology; however based on the known advantages of MSC

60 technology, potential applications and tradeoff with other renewable energy generation
61 technologies are discussed.

62 63 **Principles and performance of microbial solar cells**

64 The basic principles of MSCs, as illustrated in figure 1, are: (i) photosynthesis; (ii) transport
65 of organic matter to the anode compartment; (iii) anodic oxidation of organic matter by
66 electrochemically active bacteria; and (iv) cathodic reduction of generally oxygen. We have
67 categorized the MSCs below according to the way solar energy is captured and the mode of
68 organic matter transfer: the higher plant with rhizodeposition (PMFC); the phototrophic
69 biofilm with diffusion; and the photobioreactor or coastal marine ecosystem, which use
70 pumps for translocation. The in-depth bio-electrochemical principles of all systems are yet to
71 be fully revealed [3, 7, 12, 20-26]. Table 1 gives an overview of recent developments on MSC
72 performance and efficiency.

73 74 *Plant microbial fuel cell*

75 MSCs with living higher plants are called plant microbial fuel cells (PMFCs) [12]. With
76 PMFCs, the plant's roots directly fuel the electrochemically active bacteria at the anode by
77 excreting rhizodeposits [12, 14-19]. Rhizodeposition of plant roots is the excretion of organic
78 compounds into the soil, including sugars, organic acids, polymeric carbohydrates, enzymes
79 and dead-cell material. The rhizodeposits account for approximately 20–40% of the plant's
80 photosynthetic productivity, and these compounds can be degraded by a mixture of
81 microorganisms [25]. When the plant is growing with its roots in the MFC, electricity is
82 continuously generated *in situ*. The first published PMFC study estimated that 21 GJ/ha/year
83 (67 mW/m²) net power generation is theoretically possible under Western European (i.e.
84 Netherlands, Belgium, France) climate conditions^[12]. This net yield is on par with

85 conventional biomass electricity production systems, including digestion of energy crops
86 which achieve net power generation of 2.8 to 70 GJ/ha/year (based on: biogas production of
87 160-400 GJ CH₄/ha/year^[27]; gas combustion efficiency of 25%^[28]; and energy input of
88 30%^[29]) and biomass combustion which achieves net power generation of 27 to 91
89 GJ/ha/year (based on: biomass productivity of 8–12 ton dry weight/ha/year; heating value of
90 18-20 GJ/ton; biomass combustion efficiency of 20-40% and energy input of 5%^[30]). The
91 theoretical power output of 21 GJ/ha/year for the PMFC is a relatively conservative
92 estimation since a multidisciplinary European research consortium (www.plantpower.eu)
93 estimated that the power output of the PMFC may reach 1,000 GJ/ha/year (see explanation in
94 Box 1).

95 Three PMFC studies have integrated the anode in the sediment in which plants were
96 growing ^[14, 15, 18]. In these studies, rhizodeposits from plants and organic matter from the
97 sediment were available for generating a current. It was found that introduction of growing
98 rice plants in a MFC resulted in a sevenfold increase power output as compared to the
99 sediment MFC ^[14]. Outdoor experiments in Japan were also performed in a rice paddy field
100 ^[15, 18]. However, in these cases, power output was not higher than reported for a sediment
101 MFC without plants ^[15, 31]. The difference in power output between the rice paddy
102 experiments and the sediment MFC experiment may be due to a variety of factors, including:
103 the presence of rice plants, the sediment composition, the microbial species and the fuel cell
104 design ^[32].

105 The average power density (PD) over the operation time (OT) of 33 days of the
106 PMFC with the plant *Spartina anglica* was 50 mW/m². Of all reviewed varieties of MSCs,
107 the *Spartina anglica* PMFC study achieved the highest long-term current and power density
108 ^[16].

109 The microbial community at the anode PMFCs was analyzed to unravel the principles
110 and performance of PMFCs. It was shown that the most common bacteria were from the
111 families *Desulfobulbus* or *Geobacteraceae*^[19] or were closely related to *Natronocella*,
112 *Beijerinckiaceae*, *Rhizobiales* and *Rhodobacter*^[15]. It has been proven that species of some of
113 these families, like *Geobacter sulfurreducens*, are electrochemically active^[33]. However, it
114 has not been shown whether electrochemical active species were indeed present and active in
115 a PMFC.

116 117 *MSCs with phototrophic biofilms*

118 Solar energy is converted to electricity by growing a phototrophic biofilm on the anode of the
119 fuel cell (Table 1)^[13, 21, 34-37]. These MSCs with phototrophic biofilms have self-organizing
120 biofilm containing *Chlorophyta* and/or *Cyanophyta* and can operate for sustained periods of
121 more than 20 days^[36]. All studies to date have used mixed microbe populations, which likely
122 includes electrochemically active bacteria. A exception is one study in which a pure culture
123 of *Synechocystis PCC-6803* was applied to generate an electrical current^[21]. This
124 cyanobacterium is able to form electrically conductive nanowires when cultivated under
125 carbon dioxide limitation and excess light. As such, *Synechocystis* may be used for
126 transferring electrons from the microorganism to the anode^[21, 38].

127 Some of the MSCs include sediment, which provides additional organic matter. One
128 of these studies estimated that the 2.5-cm-thick marine sediment applied, contained enough
129 organic matter to operate the system for 22 years^[37]. To date, the theoretical output for a
130 MSC with a phototrophic biofilm has not been estimated. Based on the primary carbon
131 production of benthic biofilms of 250 g/m²/year in The Netherlands, an MFC energy recovery
132 of 60% and glucose as the carbon composite^[39, 40], we have estimated a maximum power
133 output of 61 mW/m²^[36, 37]. This value is on the same order of magnitude as the PMFCs^[12].

134 The average power density of MSCs with phototrophic biofilms was maximal 7 mW/m^2 –
135 sevenfold lower than best PMFC and 11% of the estimated maximum of MSCs with
136 phototrophic biofilms (Table 1) ^[16, 37].

137 138 *MSCs with photobioreactors*

139 MSCs can use photobioreactors to harvest solar energy via photosynthetic microorganisms
140 like algae ^[21, 41-43]. Figure 2 shows an example of a MSC with a photobioreactor and an
141 anaerobic digester. Here, the digester pre-treats the photosynthetic metabolites and
142 microorganism before supplying them to the MFC ^[42]. Photobioreactors with algae can
143 achieve PAR (photosynthetic active radiation; spectral range of solar radiation from 400 to
144 700 nm which can be used by micro algae for photosynthesis) photosynthetic efficiencies of
145 15%. With a MFC energy recovery of 29%, a power production of $2,806 \text{ mW/m}^2$ is
146 theoretically possible under Western European climate conditions ^[41, 44]. The best results have
147 been achieved with *Chlorella* in a photobioreactor, where a photosynthetic efficiency of 6.3%
148 (PAR-based) was reached. With a power conversion efficiency (PCE) of 0.04% this system
149 most effectively converted light energy into electricity of all reviewed MSCs (Table 1). This
150 resulted in 14 mW/m^2 average power production, which was only 0.5% of the theoretical
151 maximum ^[41]. It is important to note that, for the production of photosynthetic metabolites in
152 photobioreactors, energy is needed for mixing and removing oxygen up to values of 10 W/m^2
153 ^[41]. Thus, with the current state-of-the-art, MSCs with photobioreactors will have no net
154 electricity production.

155 156 *MSCs with coastal marine ecosystem*

157 MSCs may be integrated into the coastal marine ecosystem ^[45]. This ecosystem uses solar
158 energy and produces phytoplankton like macro-algae and zooplankton that float in the ocean.

159 By harvesting these kinds of substrates electricity can be generated by a MFC [43, 45, 46]. In a
160 'real life' implementation, it was envisioned that pumps could be used to feed raw seawater
161 to a 40-km-long, tubular MFC to generate electricity [45]. It has been estimated that MSCs at
162 coastal zones, which account for 10% of the ocean, can generate electrical power of 2.4 to 16
163 TWh/year which is, or when divided by the surface area, 0.01-0.05 mW/m² [45, 47]. This power
164 density is more than a factor 1,000-fold less than MSCs that use higher plants or phototrophic
165 biofilms. Analysis of current state-of-the-art, estimates that the energy input is 18 times more
166 than the electricity output [45].

167 **Challenges towards improvement of energy recovery**

168 Reviewing the most recent expectations for theoretical power generation and the achieved
169 performances in the previous section, it is clear that PMFCs and phototrophic biofilms have
170 the highest power generation (50 and 7 mW/m², respectively) [16, 37] and highest estimated net
171 power potential (67 and 61 mW/m², respectively). This makes PMFCs and phototrophic
172 biofilms the most promising MSC systems. Overall, MSCs are robust, with operating times in
173 the range of 5-175 days (Table 1) [14, 36]. In contrast, other MSCs use chemical catalysts
174 which poison the system within hours and are thus not self sustaining [48-51]. MSCs with
175 catalysts generate fuels *in situ*, such as hydrogen, which are oxidized via conventional fuel
176 cells.
177

178 The important question is: How can the power density be increased to obtain a cost-
179 effective MSC? This question can not be answered yet, because all MSCs developed to date
180 are lab-scale systems and are not designed for scale-up. In addition, insufficient and too
181 incomplete data are available for all major processes, which precludes accurate calculations.
182 For example, there are no measured data available on the coulombic efficiency (CE; fraction
183 of electrons from total oxidized electron donor which are transferred to the anode) in MSCs.

184 Currently, it is experimentally challenging to determine the exact carbon and electron fluxes
185 and, therefore, the CE.

186 However, MSC performance may be improved in pursuit of the estimated maximums,
187 as there are many approaches possible to increase the power density. There are many
188 parameters that determine the power density of MSCs. Some parameters are comparable to
189 those identified within the MFC research field and can be optimized using the same
190 principles. For example, fuel cell performance can be improved by lowering internal
191 resistances (IR), which are between 10 and 1800 Ω (Table 1). In the following paragraphs,
192 we have highlighted specific MSC studies to highlight specific challenges and opportunities
193 for improving power output.

194 195 *Increase substrate flux from photosynthetic to electrochemically active organisms*

196 It has been observed that MSCs, such as the PMFC, can be substrate-limited ^[16], suggesting
197 that the anode compartment comprising electrochemically active bacteria can oxidize more
198 organic matter (i.e. electron donors) than supplied. Thus, improving substrate flux of easily
199 biodegradable exudates, for example via an increase of rhizodeposition, will likely enhance
200 the overall energy recovery of the PMFC. Literature reveals several mechanisms toward
201 enhancing rhizodeposition ^[52, 53]. The choice of plant plays a major role in the quantity and
202 composition of rhizodeposits ^[25, 54]. The MSCs in Table 1 have current densities that are
203 considerably lower than conventional MFCs, which achieve values up to 6.5 A/m² ^[40, 55].
204 Although substrate flux does not solely determine the current density, we expect from the
205 values shown in Table 1, that several MSCs face substrate limitation. Complex substrates can
206 become more available to electrochemically active microorganisms via pre-treatment (e.g.
207 hydrolysis) of complex electron donors ^[42, 55]. In one study using an anaerobic digester and a
208 MFC, the algae suspension was partly digested into methane and the remaining substrate was

209 fed to the anode of the MFC ^[42]. Applying first a hydrolysis stage, instead of an anaerobic
210 digestion, followed by feeding to the anode of the MFC, might make more electron donors
211 available for electrochemically active microorganisms ^[42].

212 Improvement of substrate availability is also needed to operate MSCs for prolonged
213 periods at the maximum PD. MFC power output can be increased by bringing the external
214 resistance close to the internal resistance of the system ^[56, 57]. However, this route towards
215 maximizing power output is only effective when substrate flux of the system is increased as
216 well ^[56]. Within a PMFC, it was shown that an optimization strategy of lowering external
217 resistance to be equal to internal resistance was unsuccessful, possibly owing to substrate
218 limitation ^[16, 17]. The same study showed that, based on maximum PDs compared to average
219 PDs, a successful maximization strategy could lead to a 10-fold increase in power output ^[17].

220 *Reduce oxidation state of organic matter derived from the photosynthetic organism*

221 MSCs use a wide variety of electron donors, including both easily biodegradable, low-
222 molecular-weight substances as well as slowly biodegradable cellulose materials. Many of
223 these electron donors can be converted in MFCs ^[58-61]. The amount of electrons that can be
224 derived from the electron donor depends on the individual oxidation state of the substance.
225 Therefore, by controlling the kind of electron donor mobilized by the photosynthetic
226 organisms, and, with that, the oxidation state of the electron donor, energy recovery can be
227 improved in the MSC. For example, several plants increase the release of low molecular
228 weight compounds, such as sugars, amino acids and phenolics, under iron- or zinc-limitation
229 conditions ^[52]. The remaining challenge is to control the plant exudation in such a way that
230 more reduced compounds are excreted.
231

232 *Increase CE of organic matter oxidation at the anode*

233

234 The presence of other electron acceptors near the anode possibly negatively affects the CE of
235 photosynthetic metabolites in MSCs. Photosynthetic metabolites may be oxidized by mixed
236 cultures using oxygen (aerobic degradation), nitrate (nitrification), sulfate (sulfate reduction)
237 or carbon dioxide (methanogenesis) as a final electron acceptor instead of the anode, which
238 leads to a reduction in the CE ^[11, 62, 63]. An important source of alternative electron acceptors
239 in several MSC studies are nutrient media for plants and microorganisms containing
240 substantial amounts of alternative electron acceptors, such as nitrate and sulfate ^[12, 14, 16, 17].
241 Such electron acceptors can be replaced by more reduced components, thereby potentially
242 increasing the CE ^[12, 14]. Oxygen is also a relevant alternative acceptor within PMFCs. Plant
243 roots excrete oxygen, which can be used by the microbial population present or can produce
244 internal currents. In the latter case, oxygen is reduced within the anode compartment while
245 using the electrons derived from the electrochemically active bacteria present in the same
246 anode. Hence, these electrons do not flow to the cathode which thus reduces the power output
247 ^[63]. The total release of oxygen into the rhizosphere can be reduced by decreasing the average
248 root length (e.g. using *Glyceria maxima* ^[12]), because oxygen introduction into the
249 rhizosphere decreases with root length ^[64].

251 *Reduce pH gradient resistance of the fuel cell*

252 The proton production in MFCs leads to acidification in the anode compartment.
253 Accumulation of protons creates a pH gradient over the membrane, which results in a pH
254 gradient potential loss (i.e. the pH gradient resistance) ^[7, 65, 66]. This phenomenon also occurs
255 in MSCs ^[13]. Acidification has been observed in a PMFC, which could be related to current
256 generation ^[16]. Although the pH in the rhizosphere of the applied plants is generally slightly
257 acidic (5-6), reducing acidification will increase the energy recovery of this and other MSCs
258 ^[16]. Several measures have been proposed to reduce acidification in MFCs, which can be

259 translated to MSCs [7, 67, 68]. However, one must pay attention to the necessary energy input,
260 since using buffer or circulation thereof costs energy and therefore may diminishes the net
261 power production.

262 263 *Reduce transport and ionic resistance of the fuel cell*

264 The total internal resistance of MSCs is a result of pH gradient resistance, anode resistance,
265 cathode resistance, and ionic and transport resistance. These values have been calculated for
266 PMFCs [16, 66]. Ionic resistance was reduced by using a salt marsh species, thereby enabling
267 current generation at higher ionic strengths [16]. In that salt marsh species MSC study, it has
268 been observed that transport resistance accounts for the largest fraction of the total internal
269 resistance [16]. This was due to the fact that the anolyte was a stagnant water layer with an ion
270 concentration gradient. This had to be overcome in order to drive cations from the anode to
271 the cathode. Mixing of the anolyte or circulation of the catholyte over the anolyte will break
272 down the concentration gradient of cations and anions, and thus reduce the transport
273 resistance.

274 275 *Reduce anode and cathode resistance of the fuel cell*

276 Similar to MFCs, MSCs have a specific anode and cathode resistance that can be reduced to
277 improve energy recovery. General approaches, like increasing the anode surface area to
278 reduce resistance, can be derived from studies on similar bioelectrochemical systems [3, 8, 40,
279 69] which have been reviewed elsewhere [8][3][40], .

280 MSCs with oxygen reduction on graphite show poor performance because cathode resistance
281 arises from charge and mass transfer resistance [3, 70, 71]. Mass transfer resistance can be
282 reduced by using air-cathodes, however, long-term operation of air-cathodes may be
283 challenging because oxygen transport could be hindered by precipitates at the electrode, as

284 shown in bio-cathodes ^[72]. Cathode resistance can also be reduced by increasing the surface
285 area of the electrode or by enriching the cathode with a biofilm (so-called ‘bio-cathodes’) ^{[3, 41,}
286 ^{70, 73]}. Bio-cathodes use populations of microorganisms or isolates that catalyze the reduction
287 of oxygen or other electron acceptors, like manganese or iron ^[70, 74-77].

288 The charge transfer resistance can also be decreased using an electro-catalyst like
289 platinum – a solution that has been demonstrated in several MSCs ^[21, 34, 43, 69]. The challenge
290 here is to lower the dosage of costly Pt ^[78]. Other MSCs use ferric cyanide as a final electron
291 acceptor; this is suitable for laboratory experiments, but not feasible for large-scale systems,
292 as it needs frequent replenishment ^[69].

293 294 *Reduce energy input of MSCs with photobioreactors or with coastal marine ecosystems*

295 MSCs that use a photobioreactor or MSCs with coastal marine ecosystems require an energy
296 input of 6-10 W/m² for processing the electron donor for the MFC ^[41-43, 46]. This energy input
297 can diminish the net energy production of these MSCs ^[41, 45]. Thus, options for improving the
298 energy input efficiency include: (i) reducing the needed energy input, and (ii) improving the
299 photobioreactor productivity. Many valuable ideas on the improvement of photobioreactors
300 have been published ^[79].

301 MSCs that feed the MFC with seawater from coastal marine ecosystems are limited
302 by very dilute electron donors. These can be concentrated for higher power output ^[45],
303 however, it remains to be solved how this can be achieved with lesser energy input.

304 305 **Prospects and future applications**

306 We have shown that MSC technology is advancing, with the most promising MSCs
307 employing higher plants or phototrophic biofilms. The basic principles of MSCs have been
308 demonstrated; now it is time to improve the systems for ‘real life’ applications. Compared to

309 conventional solar cells, MSCs have some attractive properties that warrant further
310 development and will influence future applications of this technology ^[80]:

- 311 • MSCs can produce not only electricity, but also a wide range of fuels and chemicals;
312 this means that energy carriers both fuels and electricity can be supplied, in contrast to
313 solar cells which solely generate electricity ^[3].
- 314 • PMFCs can be easily incorporated into landscapes or into urban areas where it
315 “greens” the city. For example, PMFCs can be combined with green roofs to create
316 electricity-producing green roofs powering up to a third of a modern household (Box
317 2).
- 318 • Both the photosynthetic and electrochemical reactions are carried out by a
319 continuously growing population of microorganisms. This makes the system capable
320 of self-repair, conferring a longer lifetime and low maintenance.
- 321 • Another advantage of using of reproducing organisms is that there is no need for
322 special catalysts, like Cd, that are either costly or toxic ^[80]. Thus the MSC can be
323 applied in natural surroundings with no risk of pollution.
- 324 • MSCs have organic material as intermediate energy carriers between the
325 photosynthetic and the electrochemical portions of the cell. This organic material
326 accumulates in the MSC, therefore allowing electricity generation in the dark ^[12, 13, 41].
- 327 • Closed MSC systems can preserve nutrients for the organisms, which enable long-
328 term, low-maintenance power production.
- 329 • Integrated PMFCs can add value to other applications, such as greenhouses with food
330 or flower production, or rice paddy fields with rice production ^[14, 15]. Additionally,
331 wastewater and surface water treatment can be integrated into PMFCs to supply extra
332 organic matter for energy production ^[3, 12].

333 Currently, there are promising possibilities for application of MSCs according to the best
334 long-term power output of 50 mW/m² (Table 1). Meteorological sensors for temperature,
335 pressure and humidity installed on a buoy which requiring 24 mW were powered by a
336 sediment MFC ^[81]. We expect that these sensors and other low power requiring applications
337 like LED lights can be powered by MSCs.

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573 **Box 1. Electricity generation potential of plant microbial fuel cells**

574 A first estimate for the realistic electricity production of PMFC under Western European
575 conditions was 21 GJ/ha/year (67 mW/m²)^[12]. This estimate was based on: (i) the average
576 solar radiation of 150W/m² in Western Europe (e.g. Netherlands, Belgium, France); (ii) an
577 average photosynthetic efficiency of 2.5%; (iii) a common rhizodeposition of 40%; (iv) a
578 rhizodeposit availability for microorganisms of 30%; and (v) a microbial fuel cell energy
579 recovery of 29%, including a growth season of 6 months^[12]. This potential was according the
580 technological state-of-the-art in 2008, using general data on the conceptual process steps of
581 the PMFC.

582 In 2010, a PMFC using *Spartina anglica* reported a long-term power generation of 50
583 mW/m²^[16]. Extrapolating these results to a 6 month growth season, 25 mW/m² could be
584 produced on a yearly basis, accounting for 37% of the estimated maximum. Today, a
585 multidisciplinary European research consortium (www.plantpower.eu) is working towards an
586 optimal electricity production of 1,000 GJ/ha/year (3.2 W/m²). This value is based on the
587 highest reported data of the conceptual process steps. With an average solar radiation of 150
588 MW/km² in Western Europe^[82], increased photosynthetic efficiency of 5%^[24], a majority
589 (70%) of photosynthates transported to the soil^[83], and a possible 60% energy recovery by
590 the MFC^[40] of these photosynthates, the 3.2 W/m² power output would be possible.

591 For application in natural conditions, it was expected that 50% (1.6 W/m²) can be
592 harvested. Of course, it is recognized that these numbers are all dependent on the system
593 constituents, the environmental conditions, and time course of the experiment. Moreover,
594 challenges mentioned in this review have to be surmounted. Nevertheless, it shows that there
595 is room for optimization to achieve higher power output. The primary challenge is to further
596 understand the principle processes of PMFCs in order to subsequently design and operate

597 PMFCs with higher power outputs. With further knowledge, mechanistic models can provide
598 future estimates of power generation ^[84].

601 **Box 2. The electricity-producing green roof**

602 One of the most promising applications for the PMFC is the green roof, because it can
603 combine the advantages of these roofs with electricity generation by the PMFC. Green roofs
604 are implemented all over the world, especially in cities, and offer a myriad of advantages: (i)
605 storm-water run-off retention; (ii) high aesthetical value; (iii) increased biodiversity; (iv) air-
606 quality improvement; (v) building insulation; and (vi) urban heat island mitigation (reduction
607 of temperature within cities which have higher temperatures than rural surrounding areas) ^{[9,}
608 ^{10, 85]}. When applying a PMFC on these green roofs, decentralized electricity production can
609 be added to these advantages. On a flat roof of 50 m² – a reasonably sized roof in the
610 Netherlands – 150 W could be continuously produced when the proposed maximum of 3,2
611 W/m² is reached (see Box 1). Assuming an average electricity need of 500 W ^[86] the green
612 roof could provide about one-third of the household's electricity need. It can be expected,
613 though, since energy use of the household will decrease thanks to the insulation capacity of
614 the green roof, the PMFC power would account for a larger share of households energy need.
615 At an electricity price of 0.25 €/kWh, a 50-m² electricity-producing green roof could
616 potentially save a household € 330 per year.

617 To integrate the PMFC with a green roof, several bottlenecks still have to be
618 overcome. As the plants in a PMFC need to be submerged, water retention on the green roof
619 becomes more important. Consequently, the weight of the roof will increase, which might
620 require a fortified building construction. Moreover, current laboratory set-ups are built with a
621 lot of materials, leading to high costs associated with a scaled-up system. Detailed design of

622 the electricity producing green roof is therefore very important as it will determine both the
623 weight and the costs of the system. The current state of this technology does not enable us to
624 propose a specific design yet. Regardless of the challenges, the integration of the PMFC with
625 a green roof offers the opportunity of producing electricity at the consumer, while improving
626 the quality of the urban environment.

627 628 629 **Box 3: Trade-off between PMFCs, wind turbines, and solar panels**

630 Focusing primarily on energy production, the use of PMFCs or phototrophic biofilms may be
631 an alternative for photovoltaic solar panels or wind turbines to create energy-producing
632 landscapes. As opposed to other alternative renewable electricity sources, PMFCs offer the
633 opportunity to increase both the aesthetic value and the biodiversity of such landscapes.
634 However, photovoltaic solar panels and wind turbines can achieve higher power yields; thus,
635 a cost-benefit analysis is required when considering implementation of a renewable
636 electricity technology^[87].

637 When applied in a natural environment, PMFC power yield is estimated at a
638 maximum of 1.6 MW/km² (Box 1). Whereas wind turbines could generate 5-7.7 MW/km² on
639 a typical wind farm in Europe^[88]; solar panels could generate 4.5-7.5 MW/km² under
640 Western European conditions (solar radiation: 150W/m²; PCE: 15-25%; tilted position of
641 solar panel thus uses 2.5 m² land per m² solar panel)^[80]. In summary, power output of wind
642 farms and solar farms will be 3-5-fold higher than that of PMFCs. With an increasing need
643 for electricity and in light of the European political goal of generating 20% of its energy-need
644 in 2020 from renewable sources, pressure on high-energy-yield per surface area is increasing
645^[89]. At the same time, however, environmental impact of both wind turbines (avian mortality,
646 visual impacts, noise, electromagnetic interference) and solar panels (visual impacts, loss of

647 green space and biodiversity, increasing dark surface, use of polluting metals) is large and is
648 a source of societal debate^[80, 89]. PMFCs could offer an opportunity for electricity generation
649 while sustaining the natural environment at locations where windturbines or solar panels are
650 not desirable. Future integration of PMFCs into closed systems could provide 24 hour per day
651 electricity generation, without the use of scarce materials and with nutrient preservation.

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Table 1. Performances and efficiencies of MSCs													
Category MSC	Photosynthetic organism(s)	Electron donor(s)	Microbial community	OT (days)	CDavg _a (mA/m ²)	CDmax _a (mA/m ²)	PDavg _a (mW/m ²)	PDmax _a (mW/m ²)	CE (%)	IR (Ω)	PCE (%)	Electron acceptor(s) (catalyst)	Refs.
Plant	<i>Glyceria maxima</i>	Rhizodeposits	Bacteria	67	32	153	4	67	-	525	0.01	Oxygen	[12]
Plant	<i>Oryza sativa ssp. indica</i>	Rhizodeposits	<i>Desulfobulbus</i> cluster <i>Geobacteraceae</i> Archaea	134	44	-	21	33	31	-	0.004	Ferricyanide	[14, 19]
Plant	<i>Spartina anglica</i>	Rhizodeposits	Bacteria	78	141	-	22	79	-	1800	0.01	Oxygen	[16]
Plant	<i>Spartina anglica</i>	Rhizodeposits	Bacteria	33	214	-	50	100	-	750	0.01	Ferricyanide	[16]
Plant	<i>Arundinella donax</i>	Rhizodeposits	Bacteria	112	-	-	10	22	-	-	0.001	Oxygen or ferricyanide	[17]
Plant	<i>Spartina anglica</i>	Rhizodeposits	Bacteria	154	-	-	21	222	-	-	0.001	Oxygen or ferricyanide	[17]
Plant	<i>Oryza sativa ssp. indica</i>	Rhizodeposits, Potting soil	<i>Desulfobulbus</i> <i>Geobacteraceae</i> Archaea	175	120	-	26	-	-	-	-	Ferricyanide or oxygen (bacteria)	[14, 19]
Plant	<i>Oryza sativa L. cv. Sasanishiki</i>	Rhizodeposits Rice paddy soil	<i>Natronocella</i> <i>Beijerinckiaceae</i> <i>Rhizobiales</i>	120	-	52	-	6	-	156	-	Oxygen	[15]
Plant	<i>Oryza sativa L. cv. Satojiman</i>	Rhizodeposits Rice paddy soil	Bacteria	-	-	163	-	14	-	-	-	Oxygen (Pt)	[18]
Phototrophic biofilm	Filamentous <i>Cyanophyta</i> <i>Chlorophyta</i>	Metabolites of photosynthetic microorganism	Filamentous <i>Cyanophyta</i> <i>Chlorophyta</i>	8	-	115	-	5.9	-	10	-	Oxygen (Pt)	[34]
Phototrophic biofilm	Filamentous <i>Cyanophyta</i> <i>Chlorophyta</i>	Metabolites of photosynthetic microorganism	Filamentous <i>Cyanophyta</i> <i>Chlorophyta</i>	20	-	5	-	0.2	-	212	-	Oxygen (Pt)	[21]
Phototrophic biofilm	<i>Cyanophyta</i> <i>Chlorophyta</i>	Metabolites of photosynthetic microorganism	<i>Cyanophyta</i> <i>Chlorophyta</i> <i>Trinema</i> Bacteria	22	6	105	2	41	-	102	0.001	Ferricyanide or oxygen (bacteria)	[13]
Phototrophic biofilm	<i>Chlorophyta</i>	Metabolites of photosynthetic microorganism	Bacteroidetes <i>Chlorophyta</i> <i>Alphaproteobacteria</i> <i>Betaproteobacteria</i>	9	40	86	0.3	84	-	1300	-	Oxygen (Pt)	[35]
Phototrophic biofilm	<i>Cyanophyta</i> <i>Chlorophyta</i>	Metabolites of photosynthetic microorganism	-	5	-	0.3	-	0.001	-	-	-	Oxygen	[36]
Phototrophic biofilm	<i>Cyanophyta</i> <i>Chlorophyta</i>	Metabolites of photosynthetic microorganism and/or sediment	<i>Cyanophyta</i> <i>Chlorophyta</i> Bacteria	> 20	-	13	-	1.4	-	-	-	Oxygen	[36]
Phototrophic biofilm	<i>Chlorophyta</i>	Metabolites of photosynthetic microorganism and/or sediment	<i>Chlorophyta</i>	> 7	48	96	7	14	-	-	-	Oxygen	[37]
Phototrophic biofilm	<i>Synechaocystis PCC-6803</i>	Metabolites of <i>Synechaocystis PCC-6803</i>	<i>Synechaocystis PCC-6803</i>	18	-	5	-	0.5	-	343	-	Oxygen (Pt)	[21]
Photobio-reactor	<i>Chlorella</i>	Metabolites of <i>Chlorella</i>	Bacteria <i>Chlorella</i>	161	77	210	14	110	3	33	0.04	Ferricyanide	[41]
Photobio-reactor Digester	<i>Chlorella</i>	Effluent of digested micro algae	<i>Chlorella</i>	58	2	26	0.1	1	40	-	-	Oxygen	[42]
Photobio-reactor ^b	<i>Chlorella vulgaris</i>	<i>Chlorella vulgaris</i>	Bacteria	5	-	2500 ^c	-	980 ^c	10-30	-	-	Oxygen (Pt)	[43]

		composite												
Coastal marine ecosystem	Phytoplankton	Metabolites of phytoplankton and zooplankton	<i>Proteobacteria flavobacterium Bacteroides</i>	50	-	328 <i>c</i>	-	17 <i>c</i>	14	-	-	-		[46]
Coastal marine ecosystem**	<i>Ulva lactuca</i>	<i>Ulva lactuca</i> composite	Bacteria	7	-	2000 <i>c</i>	-	760 <i>c</i>	7-20	-	-	Oxygen (Pt)		[43]

658 *a*Geometric photosynthetic surface area (m²).

659 *b*Electron donor was produced external.

660 *c*Geometric anode electrode surface area (m²).

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663 **Figure captions**

664
665 **Figure 1.** Model of the microbial solar cells cell including the basic principles: (i)
666 photosynthesis ($6 \text{ CO}_2 + 6 \text{ H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{ O}_2$); (ii) transport of organic matter to the
667 anode compartment; (iii) anodic oxidation of organic matter by electrochemically active
668 bacteria (e.g. $\text{C}_6\text{H}_{12}\text{O}_6 + 12 \text{ H}_2\text{O} \rightarrow 6 \text{ HCO}_3^- + 30 \text{ H}^+ + 24 \text{ e}^-$); and (iv) cathodic reduction of
669 oxygen to water ($6 \text{ O}_2 + 24 \text{ H}^+ + 24 \text{ e}^- \rightarrow 12 \text{ H}_2\text{O}$).

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671 **Figure 2.** Schematic overview of a closed loop concept of a MSC with photobioreactor and
672 digester (Reprint with permission of John Wiley and Sons)^[42]; (i) photosynthesis by micro
673 algae takes place in the photobioreactor; (ii) biogas is produced from organic matter which is
674 transported from the photobioreactor to the digester; (iii) in the anode of the MFC the
675 remaining organic matter, which is transported from the digester to the anode, is oxidized by
676 electrochemically active bacteria; (v) in the cathode of the MFC oxygen, which is transported
677 from the photobioreactor to the cathode, is reduced to water.

Figure 1

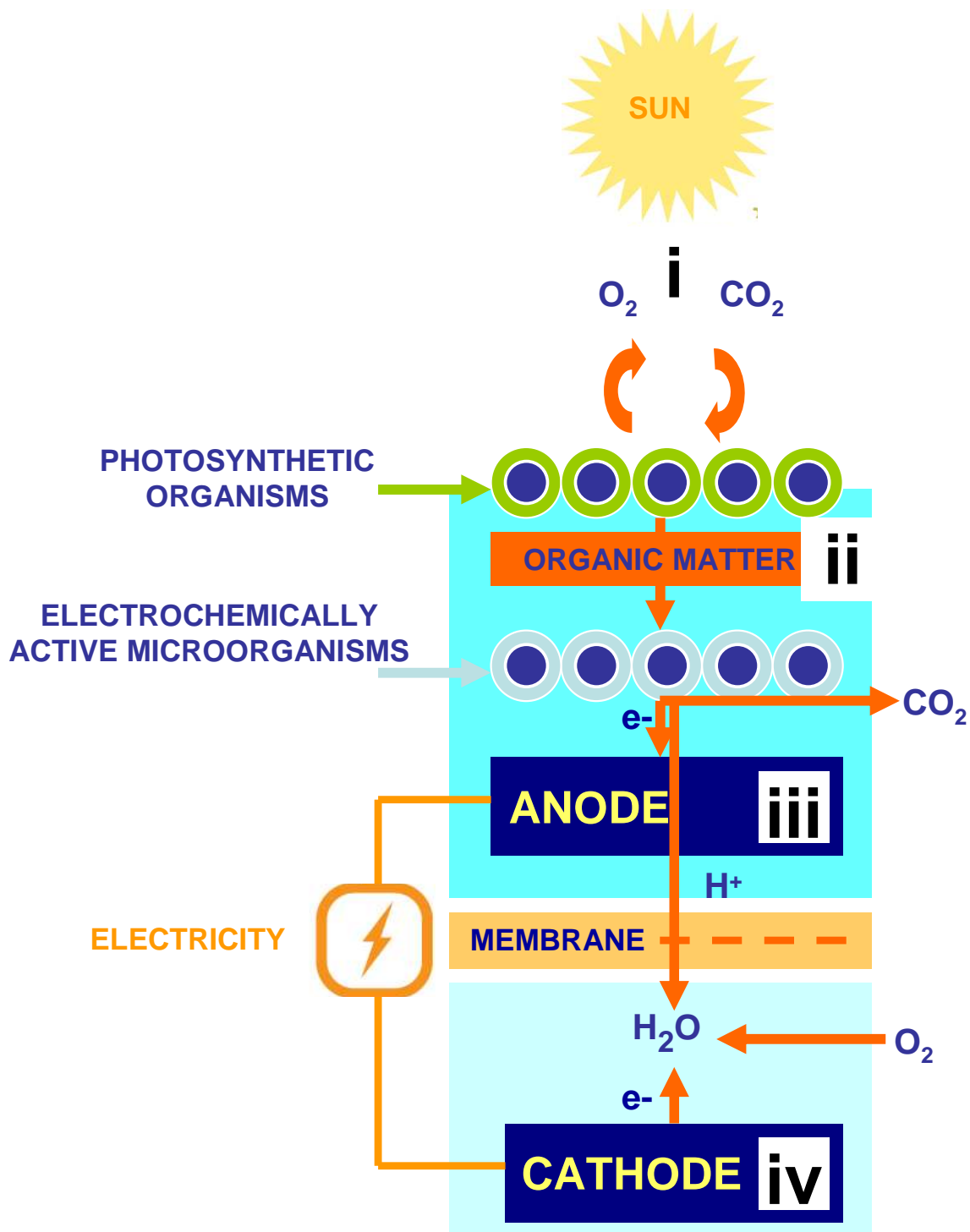


Figure 2

