



**HAL**  
open science

## Root-released organic compounds in aquaponics and their potential effects on system performance

Paula Senff, Björn Baßmann, Frederik Kaiser, Harvey Harbach, Christophe Robin, Pascal Fontaine

### ► To cite this version:

Paula Senff, Björn Baßmann, Frederik Kaiser, Harvey Harbach, Christophe Robin, et al.. Root-released organic compounds in aquaponics and their potential effects on system performance. *Reviews in Aquaculture*, 2022, pp.1-7. 10.1111/raq.12778 . hal-03944804

**HAL Id: hal-03944804**

**<https://hal.univ-lorraine.fr/hal-03944804>**

Submitted on 24 Jan 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



**There must be something in the water: Root-released organic compounds in aquaponics and their potential effects on system performance**

Journal:	<i>Reviews in Aquaculture</i>
Manuscript ID	Draft
Manuscript Type:	Opinion
Date Submitted by the Author:	n/a
Complete List of Authors:	Senff, Paula; University of Lorraine, UR AFPA Bassmann, Bjoern; University of Rostock, Aquaculture and Sea-Ranching Kaiser, Frederik; Hochschule Hof, iwe Harbach, Harvey Robin, Christophe; Université de Lorraine, Laboratory of Agronomy and Environment Fontaine, Pascal
Keywords:	Aquaponics, Integrated aquaculture, Bioactive compounds, Recirculating aquaculture, Hydroponics, Root exudates

1 **There must be something in the water: Root-released organic compounds in aquaponics**  
2 **and their potential effects on system performance**

3

4 Paula Senff <sup>1,\*</sup>, Björn Baßmann<sup>2</sup>, Frederik Kaiser<sup>3</sup>, Harvey Harbach<sup>3</sup>, Christophe Robin<sup>4</sup>, Pascal  
5 Fontaine<sup>1</sup>

6

7 1 Research Unit Animal and Functionality of Animal Products, Université de Lorraine, Vandoeuvre-  
8 Les-Nancy, France

9 2 University of Rostock, Faculty of Agricultural and Environmental Sciences, Department of  
10 Aquaculture and Sea-Ranching, Justus-von-Liebig-Weg 6, 18059 Rostock, Germany

11 3 Institute for Water and Energy Management, Hof University, Alfons-Goppel-Platz 1, 95028 Hof,  
12 Germany

13 4 Université de Lorraine, INRAE, LAE, 54000 Nancy, France

14 \*Corresponding author: paula.senff@univ-lorraine.fr; psmsenff@gmail.com

15

16

17 Optimising production in aquaponics requires in-depth knowledge of the plant, fish and microbial  
18 compartments. This opinion paper is focused on root-released organic compounds and their implication  
19 in aquaponic systems. While there has been no direct research on this to date, literature from distinct  
20 fields of study - phytochemicals in aquaculture science and root exudates in plant science - points at the  
21 novel topic of the effects of root exudates on cultured fish and the aquaculture microbiome. It shows the  
22 need for further research to better understand sources and mechanisms of such molecules and possible  
23 ways to harness beneficial effects that can guide new research directions as the role of aquaponics grows  
24 in recirculating aquaculture.

25

26 Keywords: Aquaponics, integrated aquaculture, bioactive compounds, recirculating aquaculture,  
27 hydroponics, root exudates

## 28 **Introduction**

29

30 As the aquaculture sector is facing the challenge of increasing production while reducing environmental  
31 impacts, a strategy to achieve more sustainable production systems is to move away from intensive  
32 monocultures towards polyculture systems that apply biodiversity in an agro-ecological approach.<sup>1</sup>  
33 Aquaponics, an integrated production system combining aquaculture with hydroponic plant culture,  
34 aims to move intensive aquaculture towards sustainability by recycling nutrients and optimizing the use  
35 of space and water.<sup>2</sup> In coupled aquaponics, nutrient-rich process water is circulated from an aquaculture  
36 subsystem to a hydroponic subsystem, where nutrients are taken up by plants. It is then returned to the  
37 aquaculture subsystem, minimizing water use and waste discharge. The use of pesticides can be  
38 eliminated and production sites placed closer to markets.<sup>3</sup> It is well known that plants do not only take-  
39 up molecules *via* their roots, they also release organic compounds into the rhizosphere, the medium  
40 surrounding the roots.<sup>4</sup> Bacteria settling in this area can also be influenced by root exudates. Similarly,  
41 rhizobacteria, which are closely associated with plant roots, can directly influence their environment  
42 through metabolites and/or other substances. Thus, there are many different allelopathic interactions in  
43 the rhizosphere. Furthermore, the influence of plant compounds on fish and their potential applications  
44 in aquaculture as alternatives to chemotherapy and to alleviate stress have been widely investigated and  
45 reviewed.<sup>5-7</sup> Many plant compounds that have been found to modulate fish growth, stress, or immunity  
46 can also be released over the roots. This raises the question of their potential diverse roles in a coupled  
47 aquaponics system. While to our knowledge there has been no direct research on this to date, the  
48 outcomes of some recent studies suggest there is indeed an effect on fish behavior and health while  
49 further influences on system components seem likely. We aim to synthesize the evidence that root-  
50 released organic compounds could influence the functions of an aquaponic system and argue that the  
51 subject merits further research to harness potential benefits for systems that integrate natural biological  
52 control.

53

54

## 55 **Part 1: Diversity and effects of plant root exudates**

56

57 A wide array of plants can be produced in aquaponics including leafy greens, aromatic herbs, vegetables  
58 and medicinal and ornamental plants.<sup>8</sup> Among these, especially aromatics and medicinal plants have  
59 received considerable research attention as feed-additives in aquaculture to improve growth, disease  
60 resistance and immunity (Figure 1).<sup>5</sup>

61 Plants release chemicals called rhizodeposits or root exudates into the rhizosphere in the form of high  
62 and low- molecular weight compounds. Those exudates influence a multitude of biotic and abiotic  
63 processes.<sup>4,9</sup> Root exudates include nutrients, chemoattractants or allelochemicals that interact with  
64 fungi, bacteria and other plants, to create favorable conditions and alleviate stresses on the host plant.<sup>9</sup>

65 Plants thus shape the composition of the root micro- and microbiome, inhibit the growth of pathogens  
66 and attract symbiotic i.e. nitrogen-fixing bacteria<sup>9</sup> and beneficial mutualistic arbuscular mycorrhizal  
67 fungi.<sup>10</sup> Colonization by these mycorrhizal fungi even genetically regulates nutrient transport in the root,  
68 improving nitrogen and phosphorus nutrition and subsequent plant growth.<sup>11</sup> Plants also interact with  
69 other plants *via* allelochemicals such as flavonoids, quinones, quinolines and hydroxamic acids,  
70 principally released to negatively impact metabolic processes in other plants.<sup>12,13</sup> In a few cases their  
71 effects are beneficial to the neighbor plant species through their repellent roles towards herbivores.<sup>9</sup>

72 It just seems plausible that root exudates would play a role inside the hydroponic unit of an aquaponics  
73 system as they shape the microbial communities of the rhizosphere. Especially in systems where  
74 different species of crops are produced, exuded chemicals can influence biomass production and nutrient  
75 uptake negatively or positively. Similar to findings in soil, various bacteria have been identified in  
76 aquaponics, which were associated with stimulating plant growth.<sup>14</sup> These plant growth promoting  
77 bacteria include the phyla Proteobacteria, Actinobacteria and Firmicutes as well as the genera  
78 *Acidovorax*, *Sphingobium*, *Flavobacterium* and *Pseudomonas*, genera which have been found in the  
79 rhizosphere of lettuce<sup>15</sup>; however, their role on roots and root exudates is still unknown. It has been  
80 speculated that plant roots create a beneficial environment for symbiotic microorganisms while deterring  
81 harmful bacteria by secretion of different compounds.<sup>14</sup> Organic compounds released by roots such as  
82 aldehydes, benzenoids, terpenoids and phenylpropanoids, flavonoids and coumarins have potent  
83 antimicrobial activity against pathogenic bacteria (<sup>16</sup> and references therein).

84 The bacterial community in an aquaponics system is often diverse with many different families and  
85 genera, each potentially with a specific settlement prevalence within the different sections.<sup>15,17</sup>  
86 Especially the bacteria located in a biofilter (*Nitrosomonas*, *Nitrobacter* and *Nitrospira*) are a key biotic  
87 factor in aquaponics and its nitrifying capacity is essential to the health of animals and plants. To prevent  
88 losses of nitrogen in the rhizosphere, plants exude compounds known as biological nitrification  
89 inhibitors, examples of which are gallic acid, caffeic acid and  $\alpha$ -linoleic acid.<sup>18</sup> Notably  
90 polyphenolics, but also a range of other plant compounds, have demonstrated biological nitrification  
91 inhibition (Table 1). Interactions between plants and microbes from the rhizosphere can exert a strong  
92 effect on the whole plant, and even on an ecosystem level,<sup>19</sup> with the potential to affect other organisms  
93 as well.

94

95

## 96 **Part 2: Effect of plant biomolecules on fish biology and potential pathways in aquaponics**

97

98 In the past decades, increasing attention has been paid to plants as immunostimulants and alternatives  
99 to conventional chemotherapy that reduce stress and improve fish growth and immunity when applied  
100 as feed additives or baths.<sup>5</sup> Many of the positive effects of plant additives are attributed to their  
101 polyphenol content (reviewed by <sup>20</sup>). As feed additives, they act upon the gastrointestinal tract before  
102 entering the circulatory system and being transported to other organs. They were found to stimulate the  
103 growth of beneficial gut bacteria (probiotics), thus preventing infection by pathogens. Furthermore, they  
104 can reduce oxidative stress on tissues by inhibiting the formation of or scavenging reactive oxygen  
105 species, and activating the production of antioxidant enzymes. They can also inhibit the pro-  
106 inflammatory pathways activated by exposure to such chronic stressors as animals often experience in  
107 aquaculture settings. By reducing the pathogen load in the water, phenolics and other compounds lower  
108 the risk of infection for fish.<sup>16,21</sup> Such positive effects have been attributed to a variety of molecules,  
109 many of which are not only found in the plant tissue but also in root exudates (Table 2) and they may  
110 therefore be released by the plants into an aquaponics system.

111 While the vast majority of research has focused on the addition of compounds such as polyphenols to  
112 feeds, recent studies suggest comparable positive effects on fish through external application. Most  
113 notably, in a study by <sup>22</sup>, zebrafish (*Danio rerio*) showed several improved immune parameters as well  
114 as increased survival after bacterial challenge when fish were exposed to 1 µg L<sup>-1</sup> quercetin in the water  
115 for 8 weeks. Many of the effects that were detected - increases of lysozyme, Immunoglobulin M,  
116 Myeloperoxidase, activity of superoxide dismutase and glutathione peroxidase as well as decreased  
117 malondeldehyde - have also been found in studies when quercetin was administered *via* feeding.<sup>20</sup>  
118 Effects on the innate immunity and antioxidant capacity of the intestine suggest that phenol-rich  
119 substances are ingested from the water.<sup>21,22</sup> Other possible pathways include reactivity with the gill  
120 mucus or epithelium, interaction with plasma membranes by sufficiently small molecules, and physical  
121 irritation or membrane peroxidation with low levels of continuous stress thought to have a “training”  
122 effect on defense mechanisms.<sup>21,23</sup> Additionally, small polyphenols such as resveratrol, quercetin and  
123 butein have been found to activate sirtuins, with beneficial effects on cell metabolism.<sup>24</sup> Such  
124 mechanisms are thought to be partly responsible for the improvements physiological processes and  
125 immune responses observed in fish exposed to humic substances, which are largely comprised of tannins  
126 and lignin constituents, which in turn have similar properties to plant polyphenols.<sup>23</sup>  
127 While it remains to be investigated if direct root exudates would indeed have similar effects on fish,  
128 some observations from aquaponic experiments do suggest positive outcomes. Intercropping of lettuce  
129 and red chicory, the latter known for its high polyphenol content and presence of antioxidants in the  
130 roots, resulted in higher growth of pangasius (*Pangasianodon hypophthalmus*) in an aquaponics system.<sup>25</sup>  
131 The culture of basil (*Ocimum basilicum*) in coupled aquaponics with African catfish (*Clarias*  
132 *gariepinus*) led to reduced skin lesions on the fish, suggesting less aggressive behavior.<sup>26</sup> The fish did  
133 not come into direct contact with the plants, but were kept in the same process water for several weeks  
134 without water changes.

135

136

137 **Part 3: Bottlenecks and future research**

138

139 The presence, types and concentrations of root exudates in aquaponic systems and their effect on the  
140 physiology or behaviour of fish and other farmed animals remains unexplored, and their role is only  
141 postulated based on results of feeding experiments and exposure to similar compounds (Figure 2). It is  
142 therefore relevant to investigate the production and composition of exudates in an aquaponics context:  
143 Which types of molecules are released? Do they vary between plant species? Do they remain in the  
144 water and accumulate? These are a few of the basic questions that remain to be answered.

145 Furthermore, the possible effects on the physiology and behaviour of the farmed animals are to be  
146 investigated. How do certain molecules act upon the organism? Are concentrations high or constant  
147 enough to influence animals? Can effects be measured? Do the compounds have beneficial or adverse  
148 effects?

149 Aquaponic systems vary greatly in their design and management, which may affect the types of  
150 phytochemicals released. Allelopathy between different plant species could lead to a diversity or  
151 “cocktail” of exudates and possible synergies or antagonisms between them. Furthermore, aquaponics  
152 consists of complex production systems of fish, plants and microbes. Which is the role of each biological  
153 compartment? Do root exudates influence the biofiltration capacity or other roles of the microbiome?  
154 Does the microbial community in turn influence root exudation? Are the compounds released  
155 subsequently metabolized? It remains to be seen if it can even be differentiated between the molecules  
156 released by plants and those produced by the rhizobiome.

157 In relation to these first points and going forward, the question arises if it is pertinent to manage the  
158 plant compartment of an aquaponics system with the objective to promote a “plant biodiversity” that  
159 produces vegetables for human consumption, but also achieves a biocontrol of fish welfare and improves  
160 their zootechnical performance with the objective to act at several complementary levels such as growth,  
161 immune systems and anti-stress.<sup>27</sup> suggested that there may be allelopathic interactions among different  
162 organisms within an aquaponic system. Interactions between plants and microbes from the rhizosphere  
163 can exert a strong effect on the whole plant, even on an ecosystem level,<sup>19</sup> with potential to influence  
164 other organisms. Could a certain composition of plant species achieve such agro-ecological biocontrol  
165 as crop auxiliary plants in some applications in terrestrial systems? Could such an approach integrate a  
166 control of the microbial compartment and for example limit the emergence or development of pathogens



167 such as *Aeromonas* or *Vibrio*? If we promote the establishment of plant biodiversity for the biocontrol  
 168 of fish welfare, such an approach seems easy in an intensively managed system such as a stable and  
 169 controlled monoculture, but more complex in dynamic or changing systems. Answering these questions  
 170 requires the involvement of complementary scientific skills in an interdisciplinary research approach to  
 171 enable advances in knowledge and innovation in aquaponics, at the interface of each of the different  
 172 research areas concerned.

173

174

### 175 Acknowledgements

176

177 This study was supported by the research programme Interreg GR VA Perciponie (073-4-08-191).

178

179

### 180 Tables

181

182 Table 1: Examples of vegetable crops, bioactive compounds found to be released by their roots in  
 183 hydroponics and reported nitrification inhibitory activity, “ - ” = no information available.

Plant	Compound	Concentrations found in hydroponics ( $\mu\text{mol L}^{-1}$ ) reported by <sup>28,29</sup>	Compounds has nitrification inhibitory activity summarized by <sup>18</sup>
Lettuce	Benzoic acid	0.3 – 11.5	-
	Cinnamic acid	5.8	-
	Ferulic acid	6.4 – 7.8	Yes
	Gallic acid	2.4 – 3.0	Yes
	Lauric acid	2.7 – 8.0	-
	Palmitic acid	0.75 – 12.46	-
	Phenylacetic acid	4.8 – 5.9	-
	Phthalic acid	1.9 – 14.3	-
	Salicylic acid	5.9 – 10.3	-
	Stearic acid	8.3	-
	Tannic acid	0.3 – 0.4	-
Basil	Caffeic acid	-	Yes
Cucumber	Phenylalanine	-	Yes
Tomato	Quercetin	-	Yes

184

185

186 Table 2: Examples of plant active compounds with known influence on fish physiology or water bacteria

187 load (based on reviews by <sup>6,7,30,31</sup>) found in root exudates of plants of agronomic interest.

Active compound	Effect on fish	Root exudate	Reference
Allicin	Antioxidant, antibacterial	garlic	32
Benzoic acid	Stress reducing	beans ( <i>Phaseolus vulgaris</i> , <i>Vicia faba</i> )	33
		cucumber ( <i>Cucumis sativus</i> )	34
		lettuce ( <i>Lactuca sativa</i> )	29
Cinnamic acid	Stress reducing, antiparasitic	cucumber ( <i>C. sativus</i> )	34
		eggplant ( <i>S. melongena</i> )	28
		lettuce ( <i>L. sativa</i> )	28
Epicatechin	Immunity	cucumber ( <i>C. sativus</i> )	35
Gallic acid	Immunity	lettuce ( <i>L. sativa</i> )	29
Heneicosane	Antibacterial	tomato ( <i>Solanum lycopersicum</i> )	36
Oleic acid	Wound healing	lily ( <i>Lilium davidii</i> )	37
Palmitic acid	Wound healing	lily ( <i>L. davidii</i> )	37
		lettuce ( <i>L. sativa</i> )	28
Quercetin	Immunity, antiparasitic, antibacterial	tomato ( <i>S. lycopersicum</i> )	38
Solasodine	Immunity	tomato ( <i>S. lycopersicum</i> )	38
Stearic acid	Wound healing	lily ( <i>L. davidii</i> )	37
		lettuce ( <i>L. sativa</i> )	28
Tomatidine	Immunity	tomato ( <i>S. lycopersicum</i> )	38
Vanillin	Antibacterial	lily ( <i>Lilium formolongi</i> )	39
		eggplant ( <i>Solanum melongena</i> )	34

188

189

190

191 **References**

192

193 1. Thomas M, Pasquet A, Aubin J, Nahon S, Lecocq T. When more is more: taking advantage of  
 194 species diversity to move towards sustainable aquaculture. *Biol Rev.* 2021;96(2):767-784.

195 doi:10.1111/brv.12677

196 2. Love DC, Fry JP, Genello L, et al. An international survey of aquaponics practitioners. *PLoS*  
 197 *One.* 2014;9(7):1-10. doi:10.1371/journal.pone.0102662

198 3. Joyce A, Goddek S, Kotzen B, Burnell GM. *Aquaponics Food Production Systems.*; 2019.

199 doi:10.1007/978-3-030-15943-6\_25

- 200 4. Bais HP, Broeckling CD, Vivanco JM. Root Exudates Modulate Plant—Microbe Interactions  
201 in the Rhizosphere. In: Karlovsky P, ed. *Secondary Metabolites in Soil Ecology*. Springer  
202 Berlin Heidelberg; 2008:241-252. doi:10.1007/978-3-540-74543-3\_11
- 203 5. Reverter M, Tapissier-Bontemps N, Sarter S, Sasal P, Caruso D. Moving towards more  
204 sustainable aquaculture practices: a meta-analysis on the potential of plant-enriched diets to  
205 improve fish growth, immunity and disease resistance. *Rev Aquac*. Published online 2020:1-19.  
206 doi:10.1111/raq.12485
- 207 6. Elumalai P, Kurian A, Lakshmi S, Faggio C, Esteban MA, Ringø E. Herbal  
208 Immunomodulators in Aquaculture. *Rev Fish Sci Aquac*. 2020;0(0):1-25.  
209 doi:10.1080/23308249.2020.1779651
- 210 7. Chakraborty SB, Hancz C. Application of phytochemicals as immunostimulant, antipathogenic  
211 and antistress agents in finfish culture. *Rev Aquac*. 2011;3(3):103-119. doi:10.1111/j.1753-  
212 5131.2011.01048.x
- 213 8. Maucieri C, Nicoletto C, Junge R, Schmautz Z, Sambo P, Borin M. Hydroponic systems and  
214 water management in aquaponics: A review. *Ital J Agron*. 2018;13(1):1-11.  
215 doi:10.4081/ija.2017.1012
- 216 9. Vives-Peris V, de Ollas C, Gómez-Cadenas A, Pérez-Clemente RM. Root exudates: from plant  
217 to rhizosphere and beyond. *Plant Cell Rep*. 2020;39(1):3-17. doi:10.1007/s00299-019-02447-5
- 218 10. Bouwmeester HJ, Roux C, Lopez-Raez JA, Bécard G. Rhizosphere communication of plants,  
219 parasitic plants and AM fungi. *Trends Plant Sci*. 2007;12(5):224-230.  
220 doi:10.1016/j.tplants.2007.03.009
- 221 11. Duan J, Tian H, Drijber RA, Gao Y. Systemic and local regulation of phosphate and nitrogen  
222 transporter genes by arbuscular mycorrhizal fungi in roots of winter wheat (*Triticum aestivum*  
223 L.). *Plant Physiol Biochem*. 2015;96:199-208. doi:10.1016/j.plaphy.2015.08.006
- 224 12. Callaway RM, Aschehoug ET. New and Old Neighbors : A Mechanism for Exotic Invasion.  
225 *Science (80- )*. 2000;290(5491):521-523.
- 226 13. Latif S, Gurusinghe S, Weston PA, Quinn JC, Piltz JW, Weston LA. Metabolomic approaches  
227 for the identification of flavonoids associated with weed suppression in selected Hardseeded

- 228 annual pasture legumes. *Plant Soil*. 2020;447(1-2):199-218. doi:10.1007/s11104-019-04225-4
- 229 14. Kasozi N, Abraham B, Kaiser H, Wilhelmi B. The complex microbiome in aquaponics:  
230 significance of the bacterial ecosystem. *Ann Microbiol*. 2021;71(1):1-13. doi:10.1186/s13213-  
231 020-01613-5
- 232 15. Schmutz Z, Graber A, Jaenicke S, Goesmann A, Junge R, Smits THM. Microbial diversity in  
233 different compartments of an aquaponics system. *Arch Microbiol*. 2017;199(4):613-620.  
234 doi:10.1007/s00203-016-1334-1
- 235 16. Pang Z, Chen J, Wang T, et al. Linking Plant Secondary Metabolites and Plant Microbiomes: A  
236 Review. *Front Plant Sci*. 2021;12(March). doi:10.3389/fpls.2021.621276
- 237 17. Eck M, Sare AR, Massart S, et al. Exploring Bacterial Communities in Aquaponic Systems.  
238 *Water*. 2019;11:1-16. doi:10.3390/w11020260
- 239 18. Nardi P, Laanbroek HJ, Nicol GW, et al. *Biological Nitrification Inhibition in the Rhizosphere:  
240 Determining Interactions and Impact on Microbially Mediated Processes and Potential  
241 Applications*. Vol 44. Oxford University Press; 2020. doi:10.1093/femsre/fuaa037
- 242 19. Canarini A, Kaiser C, Merchant A, Richter A, Wanek W. Root exudation of primary  
243 metabolites: Mechanisms and their roles in plant responses to environmental stimuli. *Front  
244 Plant Sci*. 2019;10(February). doi:10.3389/fpls.2019.00157
- 245 20. Ahmadifar E, Yousefi M, Karimi M, et al. Benefits of Dietary Polyphenols and Polyphenol-  
246 Rich Additives to Aquatic Animal Health: An Overview. *Rev Fish Sci Aquac*. 2020;0(0):1-34.  
247 doi:10.1080/23308249.2020.1818689
- 248 21. Lieke T, Steinberg CEW, Pan B, et al. Phenol-rich fulvic acid as a water additive enhances  
249 growth, reduces stress, and stimulates the immune system of fish in aquaculture. *Sci Rep*.  
250 2021;11(1):1-12. doi:10.1038/s41598-020-80449-0
- 251 22. Wang J, Zhang C, Zhang J, et al. The effects of quercetin on immunity, antioxidant indices, and  
252 disease resistance in zebrafish (*Danio rerio*). *Fish Physiol Biochem*. 2020;46(2):759-770.  
253 doi:10.1007/s10695-019-00750-2
- 254 23. Steinberg CEW, Kamara S, Prokhotskaya VY, et al. Dissolved humic substances - Ecological  
255 driving forces from the individual to the ecosystem level? *Freshw Biol*. 2006;51(7):1189-1210.

- 256 doi:10.1111/j.1365-2427.2006.01571.x
- 257 24. Howitz KT, Bitterman KJ, Cohen HY, et al. Small molecule activators of sirtuins extend  
258 *Saccharomyces cerevisiae* lifespan. *Nature*. 2003;425(6954):191-196.  
259 doi:10.1038/nature01960
- 260 25. Maucieri C, Id CN, Schmutz Z. Vegetable Intercropping in a Small-Scale Aquaponic System.  
261 *Agronomy*. 2017;7(63):1-14. doi:10.3390/agronomy7040063
- 262 26. Baßmann B, Harbach H, Weißbach S, Palm HW. Effect of plant density in coupled aquaponics  
263 on the welfare status of African catfish, *Clarias gariepinus*. *J World Aquac Soc*.  
264 2018;51(1):183-199. doi:10.1111/jwas.12574
- 265 27. Yildiz HY, Robaina L, Pirhonen J, Mente E, Domínguez D, Parisi G. Fish welfare in aquaponic  
266 systems: Its relation to water quality with an emphasis on feed and faeces-A review. *Water*  
267 *(Switzerland)*. 2017;9(1):1-17. doi:10.3390/w9010013
- 268 28. Lee JG, Lee BY, Lee HJ. Accumulation of phytotoxic organic acids in reused nutrient solution  
269 during hydroponic cultivation of lettuce (*Lactuca sativa* L.). *Sci Hortic (Amsterdam)*.  
270 2006;110(2):119-128. doi:10.1016/j.scienta.2006.06.013
- 271 29. Zhou C, Zhang Y, Liu W, Zha L, Shao M, Li B. Light quality affected the growth and root  
272 organic carbon and autotoxin secretions of hydroponic lettuce. *Plants*. 2020;9(11):1-16.  
273 doi:10.3390/plants9111542
- 274 30. da Cunha JA, Heinzmann BM, Baldisserotto B. The effects of essential oils and their major  
275 compounds on fish bacterial pathogens – a review. *J Appl Microbiol*. 2018;125(2):328-344.  
276 doi:10.1111/jam.13911
- 277 31. Stratev D, Zhelyazkov G, Noundou XS, Krause RWM. Beneficial effects of medicinal plants in  
278 fish diseases. *Aquac Int*. 2018;26:289-308.
- 279 32. Khan MA, Zhihui C, Xuemei X, Khan AR, Ahmed SS. Ultrastructural studies of the inhibition  
280 effect against *Phytophthora capsici* of root exudates collected from two garlic cultivars along  
281 with their qualitative analysis. *Crop Prot*. 2011;30(9):1149-1155.  
282 doi:10.1016/j.cropro.2011.04.013
- 283 33. Asaduzzaman M, Asao T. Autotoxicity in beans and their allelochemicals. *Sci Hortic*

- 284 (Amsterdam). 2012;134:26-31. doi:10.1016/j.scienta.2011.11.035
- 285 34. Chen L, Yang X, Raza W, et al. *Trichoderma harzianum* SQR-T037 rapidly degrades  
286 allelochemicals in rhizospheres of continuously cropped cucumbers. *Appl Microbiol*  
287 *Biotechnol.* 2011;89(5):1653-1663. doi:10.1007/s00253-010-2948-x
- 288 35. Zhao L, Huang Y, Hu J, Zhou H, Adeleye AS, Keller AA. 1H NMR and GC-MS Based  
289 Metabolomics Reveal Defense and Detoxification Mechanism of Cucumber Plant under Nano-  
290 Cu Stress. *Environ Sci Technol.* 2016;50(4):2000-2010. doi:10.1021/acs.est.5b05011
- 291 36. Cheng F, Ali M, Liu C, Deng R, Cheng Z. Garlic Allelochemical Diallyl Disulfide Alleviates  
292 Autotoxicity in the Root Exudates Caused by Long-Term Continuous Cropping of Tomato. *J*  
293 *Agric Food Chem.* 2020;68(42):11684-11693. doi:10.1021/acs.jafc.0c03894
- 294 37. Wu ZJ, Xie ZK, Yang L, et al. Identification of autotoxins from root exudates of Lanzhou lily  
295 (*Lilium davidii* var. unicolor). *Allelopath J.* 2015;35(1):35-48.
- 296 38. Kirwa HK, Murungi LK, Beck JJ, Torto B. Elicitation of Differential Responses in the Root-  
297 Knot Nematode *Meloidogyne incognita* to Tomato Root Exudate Cytokinin, Flavonoids, and  
298 Alkaloids. *J Agric Food Chem.* 2018;66(43):11291-11300. doi:10.1021/acs.jafc.8b05101
- 299 39. Asao T, Kitazawa H, Ushio K, Sueda Y, Ban T, Rahman Pramanik MH. Autotoxicity in some  
300 ornamentals with the means to overcome it. *HortScience.* 2007;42(6):1346-1350.  
301 doi:10.21273/hortsci.42.6.1346
- 302

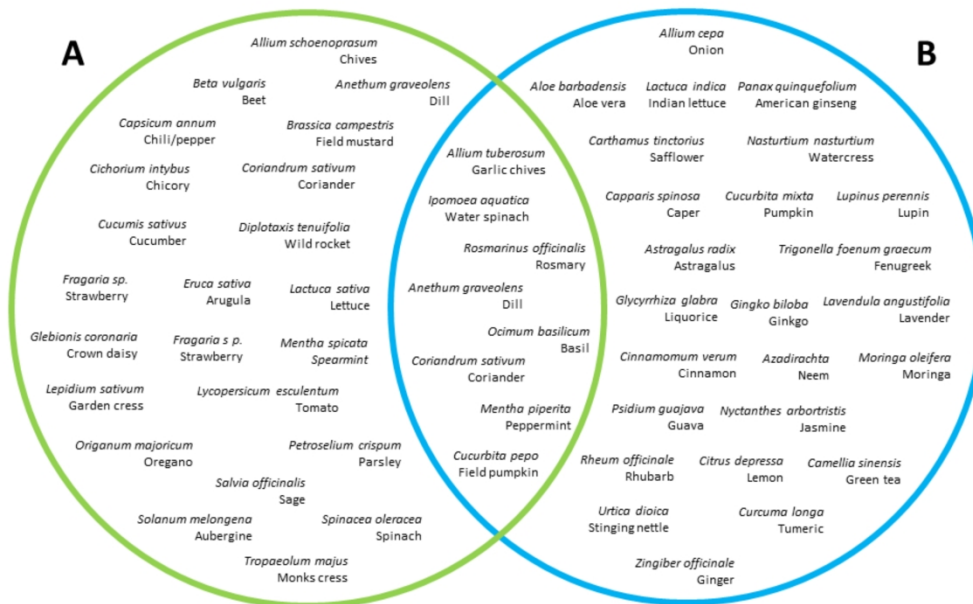


Figure 1: Overlap of (A) plants grown in aquaponics (adopted from Maucieri et al. 2018) and (B) plants investigated as aquaculture feed additives (adopted from Reverter et al. 2014, Elumalai et al. 2020), see original articles for extensive lists.

460x345mm (300 x 300 DPI)

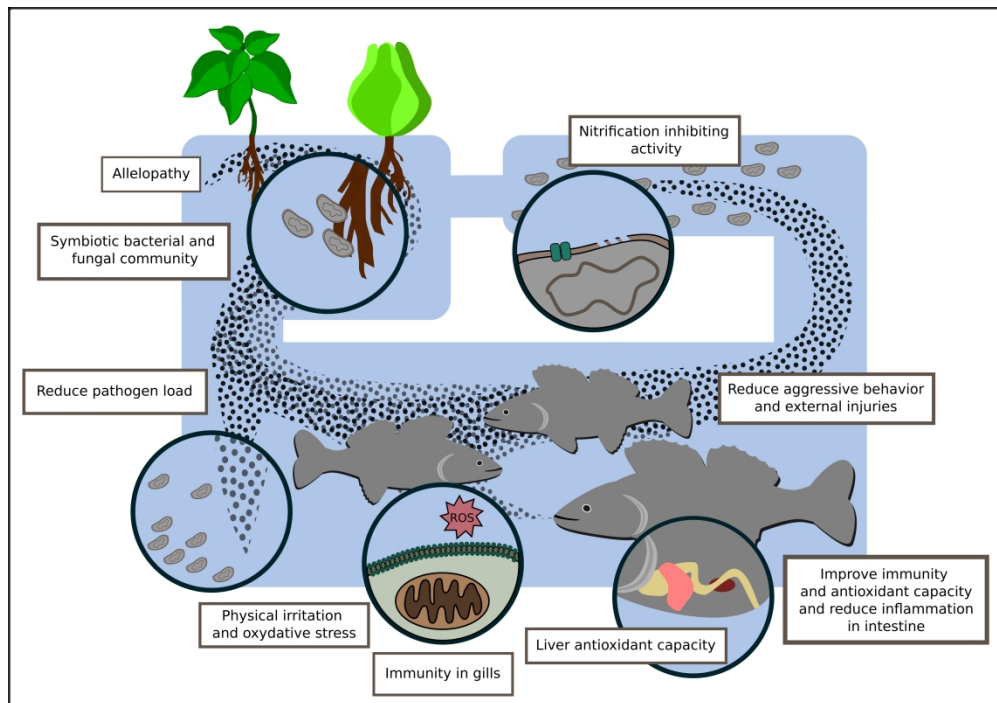


Figure 2: Possible areas of influence of root exudates in an aquaponic system.

467x327mm (300 x 300 DPI)