
This is the **accepted version** of the article:

Preece, Catherine; Peñuelas, Josep. «A return to the wild : root exudates and food security». Trends in plant science, Vol. 25, issue 1 (Jan. 2020), p. 14-21.
DOI 10.1016/j.tplants.2019.09.010

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2 **A return to the wild: root exudates and food security**
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12 **Keywords:** wild ancestors, rhizodeposition, agriculture, pesticide, fertiliser, traits.

13 **Abstract**

14 Challenges to food security under conditions of global change are forcing us to increase global crop
15 production. Focusing on belowground plant traits, especially root exudation, has great promise to
16 meet this challenge. Root exudation is the release of a vast array of compounds into the soil. These
17 exudates are involved in many biotic and abiotic interactions. Wild relatives of crops provide a large
18 potential source of information and genetic material and have desirable traits that could be
19 incorporated into modern breeding programmes. Root exudates, however, are currently under-
20 exploited. We highlight how the traits of root exudates of crop wild relatives could be used to improve
21 agricultural output and reduce environmental impacts, particularly by decreasing our dependence on
22 pesticides and fertilisers.

23 **Roots and their exudates in the fight for food security**

24 Challenges to food security (see Glossary) are forcing us to increase global crop production in order
25 to feed the growing population. The ability to provide enough food to humans around the world, in a
26 sustainable way, is endangered by a range of environmental and social factors including climate
27 change causing widespread droughts and other extreme weather events, soil erosion, changing diets
28 (such as increased meat consumption) and high food waste. An array of strategies can be implemented
29 to try to meet this task including increased cropping efficiency, closing yield gaps through improved
30 management, reducing waste and encouraging plant-based diets [1]. Characteristics of crops
31 themselves can also be modified, and the first Green Revolution increased yields by modifying
32 important aboveground traits. These ‘improvements’, however, are only possible when water and
33 nutrients are not limited, e.g. at high levels of irrigation and fertilisation. These conditions are
34 impossible for subsistence farmers and are becoming increasingly undesirable even for farmers that
35 can afford them, due to issues with sustainability and pollution [2-4]. New ideas and techniques are
36 thus needed to meet these challenges. Ecologists and plant scientists must therefore target new
37 beneficial plant traits to boost food production. Increasing the focus on belowground plant
38 characteristics may thus offer great promise [5-7]. Belowground traits vary greatly between species
39 and individuals and with environmental conditions [8, 9], so they represent a mostly unexplored area
40 in the search for tools to ameliorate the current threats to food security. Roots are the main plant
41 structures responsible for the acquisition of both water and nutrients but have largely been ignored,
42 mainly due to challenges associated with sampling within the soil [10, 11]. A wide range of traits
43 related to the roots and rhizosphere (see Glossary) could potentially be targeted to improve yields and
44 lessen the inputs of fertilisers and pesticides in the future, and attention is finally turning belowground
45 [12].

46 Root exudation remains particularly under studied. Exudation is the release of a vast array of
47 compounds into the rhizosphere, including sugars, organic acids, amino acids, secondary metabolites,
48 and structural carbohydrates [13]. Root exudates are involved in a wide range of biotic interactions

49 with other plants, microbes in the rhizosphere, and abiotic components of the soil, including nutrients
50 [14]. More specifically, root exudates can be an important source of carbon (C) for bacteria and fungi.
51 They also contain compounds that repel pathogens or attract beneficial microbes, such as nitrogen
52 (N) fixers [13]. Exudates may also increase the availability of some nutrients, such as phosphorus
53 (P), due to the release of phosphatases and chelating organic acids that render P available for plant
54 uptake [15]. Exudates can also negatively affect neighbouring plants such as through the production
55 of allelochemicals (see Glossary) [16].

56

57 **Crop wild relatives as a source of advantageous traits of root exudation**

58 Modern agriculture is centred on a very small number of crop species, but their wild relatives provide
59 a large potential source of information and genetic material [17, 18]. Understanding the processes
60 that have led to the development of modern crops can help us to understand differences in root
61 exudation due to domestication (see Glossary). Most current crops are the result of both thousands of
62 years of natural evolution and intensive selective breeding to maximise yields, leading to clear trait
63 differences from their wild relatives [19]. Crop wild relatives (CWRs) (see Glossary) have desirable
64 traits linked to mycorrhizal (see Glossary) associations [20], pest resistance [21], and tolerance of
65 challenging climatic conditions [22]. The effect of crop domestication on the provision of ecosystem
66 services, however, has not been well studied, leaving many gaps in our knowledge [23, 24], especially
67 relating to root exudation.

68 Exudation varies between species and supplies about 15% of belowground C in cereals and
69 grasses [25] and can therefore be an expensive process to maintain. Exudate production thus
70 represents a balance between the possible advantageous functions that exudates bestow on plants
71 against the loss of energy that could otherwise be allocated elsewhere. The more we learn about root
72 exudates, the clearer it becomes that they can show a high level of variation, in both amount and
73 composition, at all levels of organisation. For example, patterns of exudation vary between species
74 and individuals, but root exudation also varies within individuals over time and in response to abiotic

75 factors, such as the availability of water or nutrients [26]. Evidence suggests that the *amount* of
76 exudation increases when plants experience drought [27-29] and low P availability [30-32], although
77 results also vary depending on the experimental conditions. Exudate *composition* also varies in
78 response to the availability of nutrients such as N, P, and potassium [26, 33, 34]. Plant breeders are
79 now focusing more on CWRs to provide important new developments in the next generation of crops
80 but identifying differences in root exudation between crops and their wild relatives will be a
81 challenge. These differences may be general patterns that are repeated across plant families (e.g.
82 grasses, legumes, and brassicas) or may be much more idiosyncratic, with different, potentially
83 advantageous traits in some species but not others. The large potential benefit of these new findings,
84 combined with the current lack of knowledge in this area, will likely generate an area of great interest
85 for future research.

86 By reviewing the available literature on root exudation, we hope to identify sources of
87 variation between crops and their wild relatives and to learn how this variation may offer
88 opportunities for plant breeders to develop the next generation of crops. We will therefore discuss the
89 differences in root exudation and the interactions within the rhizosphere between crops and their wild
90 relatives. This discussion will allow us to assess the potential to identify advantageous traits of root
91 exudation in CWRs that could improve agricultural productivity and sustainability, with a focus on
92 reducing fertilisation and pesticide use. We will also discuss potential obstacles to this process, which
93 could be focal areas for improving the likelihood of success.

94

95 **Improving tolerance to pests**

96 Traits from CWRs may benefit crop breeding, in order to reduce pesticide use. Root exudates
97 participate in a wide range of positive and negative interactions with soil organisms. Primarily these
98 associations are with microorganisms in the rhizosphere [35], but important interactions also occur
99 with invertebrates [36]. Studies of plant defence generally provide support for the hypothesis that
100 crop exudates can be modified to improve pest resistance. Crops tend to have lower resistance to

101 attacks from herbivores compared with their wild ancestors [37]. This is perhaps due to direct
102 selection to remove protective but undesirable food traits, such as a bitter taste, toxicity, toughness,
103 or hairiness, and/or because breeding for increased yield has led to trade-offs with defensive
104 mechanisms [38, 39]. Domestication can reduce the level of resistance of aboveground tissues to
105 herbivores [37], for example with lower silicon concentration in the leaves of cereals [40], lower
106 foliar toughness in domesticated maize (*Zea mays*) compared with wild relatives [41], and lower
107 levels of glucosinolate defences in domesticated compared with wild cabbage (*Brassica oleracea*)
108 [42]. There are also examples of the loss, during domestication, of herbivore-induced VOCs from the
109 leaves of maize [43] and cranberry (*Vaccinium macrocarpon*) [44]. These VOCs are beneficial to the
110 plant as they attract other species that predate the herbivore. These results, however, contrast with
111 others demonstrating that two parasitoids were more attracted to domesticated kale (*Brassica*
112 *oleracea*) and scarlet runner bean (*Phaseolus coccineus*) than their wild relatives, implying that the
113 foliar VOCs of the crops had not been removed by selection during domestication [45].

114 Whether consistent reductions in root defence to pests are due to domestication remains to be
115 confirmed, but good evidence of impacts on belowground VOCs produced by plants has been found.
116 Maize commonly suffers herbivory from the larvae of the beetle *Diabrotica virgifera virgifera*, also
117 known as the Western corn rootworm. The wild ancestor of maize, teosinte (*Zea mays* subsp.
118 *parviglumis*), and European maize varieties produce and emit the sesquiterpene (*E*)- β -caryophyllene
119 from their roots, which attracts an entomopathogenic nematode that feeds on the beetle larvae. This
120 chemical signal, however, is not released by most North American maize cultivars, which are thus
121 more susceptible to beetle attack; this trait may have been lost during breeding [46, 47].
122 Reincorporation of the ability to produce this sesquiterpene can greatly benefit the productivity of
123 North American maize and is an example of a wild trait that has been successfully restored to a crop
124 [48]. This indicates the potential for using gene editing or classical breeding techniques for
125 manipulating the traits of root exudates to reduce damage by pests, thereby lowering the requirement
126 for high rates of pesticide use.

127

128 **Opportunities to reduce fertilisation**

129 Contemporary intensive farming systems use high levels of fertilisation to counteract the constraints
130 to growth due to too little soil N, P, or other elements. Reducing fertiliser use, however, is desirable
131 for environmental and economic reasons [49]. Global levels of fertilisation are higher than ever but
132 are not a completely new phenomenon. Humans became less nomadic at the beginning of agriculture
133 with the cultivation of plants, and the soils in these early settlements would have been richer in
134 nutrients compared with natural soils due to the use of human and animal waste [50]. Nutrient
135 acquisition is therefore not the main requirement in most crops that have evolved and been bred in
136 these conditions [20]. Wild species that have not been domesticated may therefore have traits that are
137 better for acquiring soil nutrients. Crop wild relatives might thus produce higher amounts of exudates
138 compared to crops, different extracellular enzymes with higher efficiency in phosphorus
139 solubilisation, and/or a higher proportion of organic anions, whereby crops would not need to invest
140 as much in mobilising mineral P. The very limited study of crops and their wild relatives, however,
141 has not yet supported this premise. The composition of exudate metabolites in one recent study
142 differed between modern durum wheat (*Triticum turgidum* subsp. *durum*), domesticated emmer
143 wheat (*T. turgidum* subsp. *dicoccum*), and wild emmer (*T. turgidum* subsp. *dicoccoides*), but the
144 pattern was not clear for organic acids, and the effects depended on the substrate in which the plants
145 were grown [51], indicating the complexity of the potential effects of domestication on exudation
146 composition.

147 Other root exudates that can directly mobilise nutrients include those involved in the uptake
148 of iron, an element that often has low bioavailability in soils. In non-graminaceous plants, rhizosphere
149 acidification combined with the release of phenolics (such as coumarins), and flavins facilitates iron
150 uptake (strategy I) [52, 53]. In grasses, chelators called phytosiderophores are exuded into the
151 rhizosphere (strategy II) greatly increasing the uptake of iron and, to a lesser degree, other

152 micronutrients such as copper, cobalt, nickel and zinc [53, 54]. Although comparisons of
153 phytosiderophore production between crops and CWRs are few, one study comparing *Triticum*
154 *aestivum* and *T. durum* with six *Aegilops* species found exudation of phytosiderophores was three to
155 four times higher in the wild *Aegilops* cultivars compared with domesticated wheat cultivars, and
156 moreover, *Aegilops* plants had higher shoot and root concentrations of iron and zinc [55]. The
157 *Aegilops* genus is closely related to bread wheat and has already significantly contributed to wheat
158 breeding [56], making this a good target for improvements relating to root exudation.

159 Examples comparing crops and CWRs are still lacking, but much evidence suggests that the
160 nutrient content of soil affects the composition of exudates [57]. Plant species from the family
161 Proteaceae notably produce different types of roots when growing in soil low in nutrients. For
162 example, white lupin (*Lupinus albus*) can grow thicker “cluster roots” (or “proteoid roots”) in the P-
163 poor soils of Australia and elsewhere [58, 59]. These roots have larger surface areas and exude higher
164 amounts of carboxylates (organic anions, disassociated forms of the organic acid carboxylic acid),
165 which are important for changing soil pH and can chelate soil minerals and mobilise P in the soil [31,
166 58]. An increase in exudation of carboxylates has been experimentally demonstrated under conditions
167 in low P soils. For example, the production of root exudates in low P conditions in an experiment
168 with sugar beet increased 4-5-fold [30]. Exudation in a study with white lupin even increased 25-fold
169 (mostly malate and citrate) when the plants were grown in low P conditions [60]. While the addition
170 of cluster roots is not possible or looked-for in all crops, greater understanding of organic acid
171 exudation in CWRs, and the potential for increasing P-mobilising abilities in crops are clearly
172 desirable.

173 Root exudates also play an important role in promoting positive interactions with
174 microorganisms, e.g. initiating colonisation with mycorrhizae by the release of strigolactones (see
175 Glossary) [61]. Evidence has already been found of differences due to domestication. Colonisation
176 by mycorrhizae was lower in breadfruit (*Artocarpus altilis*) than its wild relatives [62], and
177 mycorrhizal responsiveness (plant improvement in the presence of mycorrhizae) was lower in modern

178 than older cultivars of wheat [63]. Other studies, however, have found that colonisation by
179 mycorrhizae is not necessarily lower in domesticated cultivars [64] and that colonisation in annual
180 crops may be lower than in their wild ancestors, but new cultivars did not lack the capability to form
181 these associations and could even be more responsive to mycorrhizae than wild ancestors [65]. The
182 largest experimental study to date on this topic (Martín-Robles *et al.*, 2018) measured how
183 domestication affected mycorrhizal responsiveness in 27 crop species and their wild progenitors,
184 concluding that crops only benefitted from mycorrhizae in P-limited conditions, whereas their wild
185 ancestors benefitted irrespective of P availability [20].

186 The symbiotic relationship between plants and N-fixing bacteria is another positive
187 interaction between roots and microorganisms, with the legumes-rhizobia (see Glossary) relationship
188 being the most common example. Leguminous species cannot form symbioses with all types of
189 rhizobia, and the amount of specificity varies between plant species. Root exudation is part of this
190 process, because rhizobia are attracted to roots of suitable host plants by the release of flavonoid (see
191 Glossary) compounds in the exudates [66]. Evidence from pea, faba bean, and chickpea suggests that
192 domestication has reduced the ability of legumes to associate with many rhizobial populations,
193 leading to lower symbiont diversity compared with related wild species [67-70]. We continue to lack
194 information, however, about consistent differences in the amount or type of flavonoids released by
195 crops compared with their wild relatives. Increasing the ability of plants to take up nutrients by
196 increasing beneficial interactions with microbes is another possible route to lower the dependence on
197 fertilisers.

198

199 **Further clues of the effects of domestication on the rhizobiome**

200 We can infer information about the effects of domestication on root exudation from the differences
201 in rhizosphere microorganisms, because the rhizobiome (see Glossary) is intimately linked to and
202 shaped by root exudates [71, 72]. We can thus use knowledge about the rhizobiome as a mirror to

203 reveal changes in exudation. Edaphic factors and other C pools, though, are also very important [72,
204 73]. Abundant evidence supports divergent patterns of exudation between crops and their wild
205 relatives, in a range of species. A general pattern of reduced diversity in the crop rhizobiome has been
206 reported [70], and pot experiments with controlled soil conditions allow the observation of differences
207 due to domestication. For example, small but significant differences in the composition of bacterial
208 root microbiota have been found between wild, traditional, and modern cultivars of barley (*Hordeum*
209 *vulgare*) [74]. Bacterial alpha diversity is significantly higher in the rhizospheres of teosinte than
210 domesticated sweet corn [75], wild *Agave* than domesticated *Agave tequilana* [76], and wild beet
211 (*Beta vulgaris* subsp. *maritima*) than modern sugar beet (*Beta vulgaris* subsp. *vulgaris*) [77]. In
212 contrast, bacterial diversity is higher in lettuce (*Lactuca sativa*) than its wild relative, *L. serriola* [78].

213 Our knowledge of crop rhizobiomes generally suggests a reduction in microbial diversity due
214 to domestication. Exudates are a major source of substrates on which rhizosphere microbes feed so
215 crops may exude a less diverse array of compounds, creating a lower diversity of metabolic niches
216 for microbes to exploit [79]. Domestication has decreased the genetic diversity within crops compared
217 with their wild relatives due to the strong selection of a small proportion of the original wild
218 populations that contained favourable traits [80], and evidence suggests that this loss of diversity has
219 affected various ecological aspects of crop roots and rhizospheres. There is therefore an opportunity
220 to recover some of this lost diversity via breeding programmes with CWRs.

221

222 **Concluding remarks and future directions**

223 To date, CWRs have been used to improve many crops, especially sunflower, wheat, and
224 potato, with breeding programmes using CWRs to improve resistance to biotic and abiotic stresses,
225 increase yields, and improve fertility [18, 81]. Few programmes, if any, however, have incorporated
226 wild traits associated with root exudation. The quantity and composition of root exudates may differ
227 between domesticated crop species and their wild relatives. This research may be relatively

228 undeveloped, but it offers a range of potential benefits to future cultivars. Two key areas could be
229 exploited (Figure 1). Firstly, defence against root pests is a promising goal, through augmentation of
230 beneficial VOCs and other non-volatile secondary metabolites. There is already clear evidence
231 suggesting that VOCs from root exudates protecting against herbivory vary between maize cultivars
232 [46, 47], and indeed, the ability to emit these VOCs was successfully introduced into a non-emitting
233 maize cultivar, leading to much lower damage from a beetle pest [48]. Secondly, reducing the
234 dependence on fertilisers may be possible via two routes: (1) incorporation of traits from CWRs that
235 increase the availability of soil P, perhaps with mechanisms similar to those in Proteaceae such as
236 higher exudation of organic acids; (2) increasing positive associations with microbes, such as N-
237 fixing bacteria and mycorrhizae, because the pairing of symbionts or fungal partners of some current
238 crops may be restricted, and more beneficial partnerships could be nurtured. A third area, which we
239 have not focused on in this review, is the potential for root exudates in CWRs to have traits relating
240 to weed suppression. Although future applications for allelopathy in agriculture have been recognised
241 [82] studies on the difference in these types of allelopathic traits between crops and their wild relatives
242 are still greatly lacking and is a clear topic for future work.

243 Two main complicating factors limit the incorporation of CWR traits of root exudation into
244 crops. Firstly, perhaps the only consistent result from the different studies on root exudation is the
245 inconsistency in exudation patterns. That is, exudation varies greatly, not just at the level of the
246 individual or species, but also depending on soil type, availability of water or soil nutrients, plant age,
247 light intensity, and other factors. Moreover, differences in the growth and sampling conditions affect
248 root exudation, and this is vastly understudied. Growth conditions can vary from hydroponics, to soil
249 in pots and microcosms, to growing in the field. Sampling can be done via many different methods,
250 including direct measurements of exudates collected in solution, soil or via another type of ‘trap’, or
251 with isotope labelling, and with samples taken from a root segment or from the whole root system,
252 and with many other variations (see the review in Oburger et al. 2018 [83] for more details).
253 Identifying differences that are due to domestication and predicting how the incorporation of a new

254 trait would function outside the controlled conditions of a laboratory or greenhouse are thus very
255 complicated, and without a large effort to standardise the conditions under which exudates are
256 measured we will likely continue to struggle to draw general conclusions. The effects of
257 domestication on exudation also likely differ between crops where the seeds, fruits, or leaves are
258 consumed and crops where the roots and tubers are eaten, due to differences in above- or
259 belowground. The second challenge is that it remains difficult to reliably measure root exudation,
260 particularly in field conditions, where efforts to find reliable and serviceable methods should be
261 focused [83]. Also, regarding work investigating the composition of exudates, much of the current
262 research is based around targeted analysis, as non-targeted metabolomics analysis is currently
263 expensive both in terms of time and cost of equipment. So, it must be noticed that when only looking
264 at a small fraction of the large diversity of compounds that are released other important patterns may
265 be missed.

266 During the last decades, the replacement of locally adapted, diverse, traditional varieties with
267 cultivars bred for high productivity in intensive agricultural systems means that there is too often a
268 very limited focus on sustainability [84]. The investigation of CWRs to find possible beneficial traits
269 associated with root exudation offers many possibilities for improving both the quality of our food
270 and the agricultural practices that produce it. Efforts may first need to be focused on improving the
271 measurement of root exudation in realistic environments, but the opportunity for substantial advances
272 to improve the resilience of our food production encourages the continued search for beneficial root
273 traits in crop wild relatives.

274

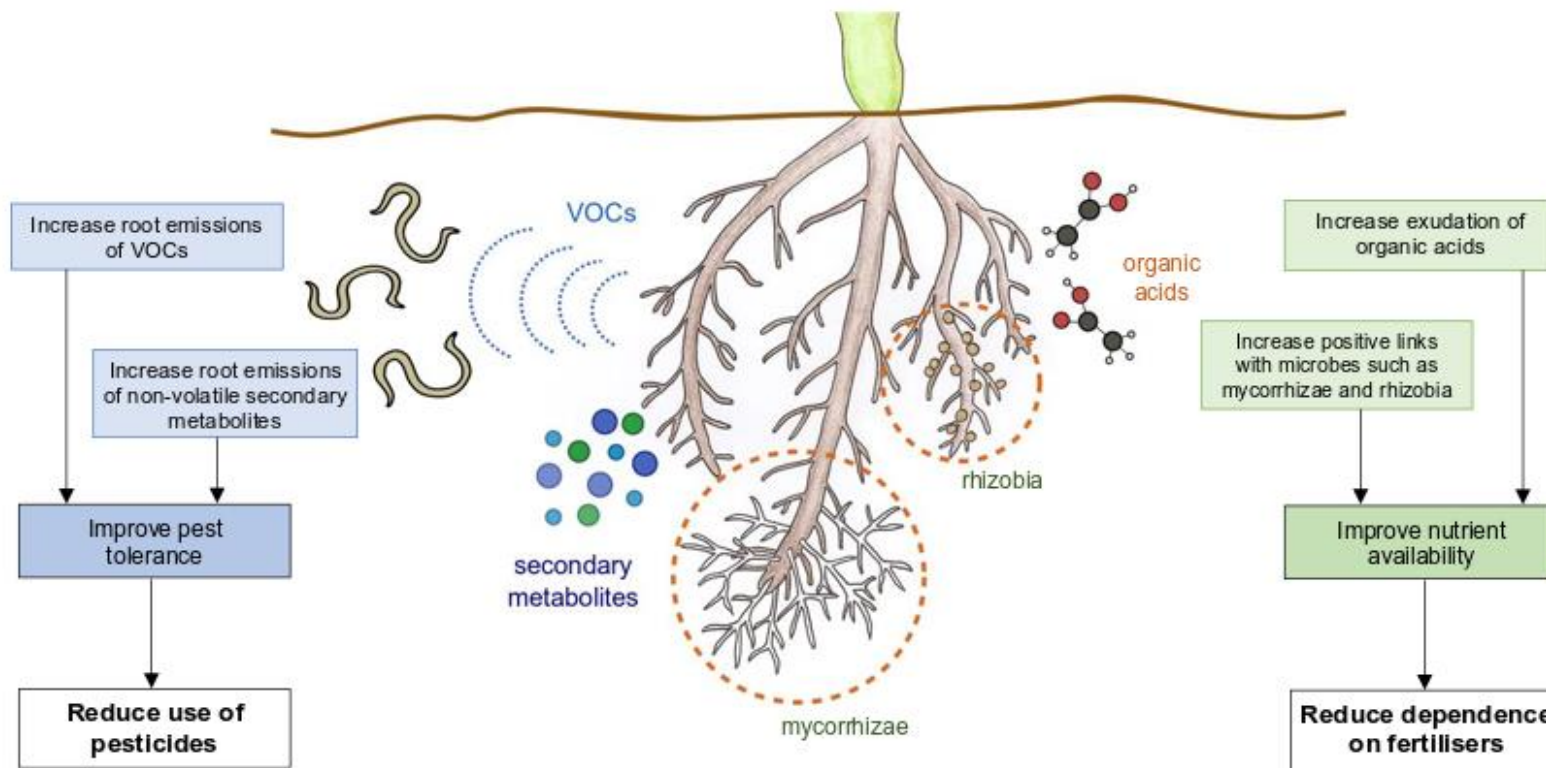
275 **Acknowledgements**

276 This research was supported by the European FP7 S-Clima project PIEF-GA-2013-626234, the
277 Spanish Government grant CGL2016-79835, the European Research Council Synergy grant ERC-
278 2013-SyG-610028 IMBALANCE-P, and the Catalan Government grant SGR 2017-1005.

279 Fig. 1. A summary of some of the beneficial traits that could be incorporated from crop wild relatives to improve agricultural practices and food
280 security. An increase in the release of volatile organic compounds (VOCs) and other non-volatile secondary metabolites (e.g., phenolics, alkaloids),
281 could attract predators of root pests or directly inhibit herbivores and weeds. This would lead to increased pest resistance, therefore reducing the use of
282 pesticides. An increase in exudation of organic acids and more beneficial associations with microbes (e.g., mycorrhizae and rhizobia) could increase
283 soil nutrient availability (especially N and P), reducing dependence on fertilisers.

284

285



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