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Woody Plant declines. What's wrong with the microbiome?

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Abstract

Woody plant (WP) declines have multi-factorial determinants as well as a biological and economic reality. The vascular system of WPs involved in the transport of carbon, nitrogen and water from sources to sinks has a seasonal activity, which places it at a central position for mediating plant–environment interactions from nutrient cycling to community assembly and for regulating a variety of processes. To limit effects and to fight against declines, we propose (i) to consider the WP and its associated microbiota as an holobiont and as a set of functions, (ii) to consider simultaneously, without looking at what comes first, the physiological or pathogenic disorders and (iii) to define pragmatic strategies including preventive and curative agronomical practices based on microbiota engineering.

Woody plants in ecosystem functioning

Plants can be simply divided into annual, biennial (life cycle from seed to seed lasts one or two years) and perennial plants (can survive more than 2 years). Woody plants (WP) are perennial plants characterized by the presence during the non-growing season of persistent aboveground dormant parts, as well as ligneous material (mainly in vascular tissues).

WPs play a major role in the functioning of the ecosystem. For example, they actively participate in water and CO_2 cycles, especially within complex ecosystems such as forests [1]. WPs render many ecosystem services, either directly when providing economically important goods and services (*e.g.* wood, fiber and fruits) or indirectly as reservoir of biodiversity [1]. In a context of global warming, their carbon (C) sequestration capacity is also of particular interest [2].

In their tissues or organs, WPs host a set of symbiotic and free-living microorganisms (*i.e.* archae, bacteria, fungi, oomycetes, protists and viruses) commonly referred to as the **microbiota**. Although biomolecular techniques for detecting the diversity of microorganisms are improving, host-microbiota interaction mechanisms are still poorly understood [3–5]. The emergence of the "**holobiont**" concept, *briefly defined as* a "functional entity formed by a macrobe and its long- and short-term associations with microbes and viruses" [6], opened the possibility to view an entire system.

In the present review, we first discuss the origin of WP declines with a focus on the link between flow and storage of carbon (C), nitrogen (N) and water in WPs and their

transfer to/from associated microbes, in healthy or declining conditions. Then, we introduce definitions and concepts about the interactions between WPs and their microbiota, often inspired by knowledge on animal-associated microbiota. Finally, we discuss prospects of microbiota engineering to enhance tolerance of WPs to declines.

Woody plant declines: pathological and physiological disorders

Decline versus dieback

In the last decades, WP declines are affecting more and more species [7]. They can be defined as a long-term degeneration of plant tissues following a succession of multiple negative events (*e.g.* abiotic stresses, climate deregulation, emergence of new pathogens, biological invasions and agricultural strategies). WP declines may also be seen as a decrease, over multiple years, of wood or fruit productivity, leading or not to a sudden death, the latter being occasionally referred to as dieback (**Box 1**). Several authors use 'decline' strictly for the progressive reduction of the vigor of the WP, whatever its causes and symptoms, while they would associate 'dieback' to the drying of the plant that starts at the tips [8]. However, the distinction between 'decline' and 'dieback' is not always made or accepted as such by forest pathologists [8,9]. For better readability, we will retain only the term 'decline' later in this review.

Origin of the declines and impact on productivity and ecosystem services

Individual tree mortality, estimated by the ICP forest network (www.icp-forests.net ; [10]), has doubled in Europe's temperate forests over the last three decades [11]. Per year, about 0.5 to 1.5% of trees died owing to different factors such as fungi, fire, grazing, climate change. Today, the impact of WP declines on ecosystem services has reached an apparent peak and brought to our attention the necessity to identify determinants and mechanisms leading to their occurrence [12]. However, the main mortality factor remains undetermined (**Box 2**).

Longevity and late sexual maturity of WPs make their physiology, development and ecology different from annual plants. WPs are especially vulnerable to pathogens since exposure lasts for a longer period of time compared to annual plants [13]. WPs are also increasingly exposed to pathogens due to silvicultural and fruit farming techniques, and

96 especially globalization, favoring fast dispersal of microbe species along commercial routes
97 [14].
98 Compared to less complex or non-multifactorial diseases, it is difficult to define a
99 state of decline based on the observed symptoms, as these vary widely according to the
100 species or individuals concerned. Declines may affect different compartments and the
101 symptoms may be diverse (*i.e.* twigs drying, leaves yellowing, wood rotting). Since declines
102 result from the combination of various factors, the association of given symptoms to their
103 origin is challenging. In most declines, the whole plant is damaged including woody parts and
104 leaves. A given decline can first appear in a specific compartment, then spread to others, and
105 finally affect the balance of the whole holobiont. After a while, it leads to visible symptoms
106 such as a significant loss of biomass as shown in poplar [15] and ash [16,17], or a decrease in
107 the quantity and quality of fruits (*e.g.* grapevine or olive tree) [18,19]. In addition to the
108 economic impact (*e.g.* loss of quality, quantity, yield), forest diseases can affect some
109 ecosystem services either directly (*e.g.* C sequestration, water purification, soil stability) or
110 indirectly (*e.g.* associated biodiversity, recreational and cultural aspects) [20,21].
111
112 *Carbon, nitrogen and water in WP declines: fueling and fluxes problems?*
113 WP species exhibit a wide range of gas exchange responses and hydraulic strategies,
114 depending on whole-tree conductance and rooting depth. Photosynthesis essentially takes
115 place in leaves during the light period. The Rubisco-fixed C is partly accumulated (i) as starch
116 in the chloroplast to sustain metabolism during the dark period and (ii) as hexoses and
117 sucrose in the cytosol for both daily metabolism and plant long distance transport. The
118 excess of C is exported for long-term storage in the trunk and roots. Within the plant,
119 carbohydrate are transported from photosynthetic and storage tissue (sources) to areas of
120 active growth and metabolism (sinks). This phenomenon is at least partially regulated by a
121 large number of monosaccharide- and sucrose-specific transporters, identified in WPs as
122 poplar and grapevine [22,23]. Besides C, nitrogen (N) is required in significant quantities as it
123 constitutes 1–5% of the WP dry weight [24]. N compounds are taken-up directly from the
124 soil either under organic or inorganic forms directly through the plant roots- or the
125 mycorrhizal-pathway. They are then transferred to the upper parts in the form of amino
126 acids *via* an interconnection of the xylem and the phloem (**Box 4**) [23,25]. Because N-

127 containing compounds are necessary for C assimilation, N mobilization and C assimilation
128 are probably tightly co-regulated to allow the optimal development of WPs [26,27].
129 C storage organs, varying depending on the season [28], play a key role in annual and
130 seasonal metabolism and growth variations in WPs [26], as it represents resources that build
131 up in the plant and can be mobilized in the future. This is especially true in deciduous species
132 where in spring remobilization of reserves is necessary for budburst and growth of new
133 leaves, allowing functional photosynthesis [29]. N is stored before leaf fall. Two thirds of the
134 foliar N, mainly as Rubisco, which is primarily a storage protein, is recycled during the leaf
135 senescence process, then transported and stored as amino acids and proteins in the
136 perennial parts of the tree [30]. C and N stored in autumn in the trunk and roots are used for
137 wood formation, especially for the phloem [31], before N root uptake is efficient.
138 As C, N and water transport depends on source and sink activity, any disturbance
139 could influence WP functions, from growth and allocation to defense and reproduction.
140 Leaves, trunks and roots perform unique functions, necessary for a healthy development.
141 Interruptions caused by short, long term or successive stresses, in any of the functions
142 performed by leaves (decrease of photosynthesis leading to less food and fewer energy
143 storage), trunks (damage to vascular tissues reduces or inhibits C, N and water transport)
144 and roots (improper soil conditions and mechanical damages lead to lesser root extension)
145 may lead to plant starvation. These interruptions, combined with defenses against other
146 diseases (physiological or pathogenic), could finally lead to decline. In addition, several
147 groups have recently proposed to link forest declines with microbiome modification or
148 imbalance [32].
149
150 **The WP holobiont**
151 The recent explosion of the number of studies on human gut microbiota highlighted
152 links between altered microbiota (dysbiosis) and development of immune-mediated and
153 metabolic pathologies such as obesity, type-2 diabetes, or cancer [33]. In this context, one
154 could imagine a transposition to the study of links between taxonomic composition and
155 functioning of the WP microbiota and decline outcomes.
156
157 *Key concepts on the plant holobiont*

158 Plants do not live alone, but are colonized and surrounded by microbes. Microbial
159 colonization, whether **epiphytic** or **endophytic**, vary between plant tissues. A wide diversity
160 of microbial taxa is involved in these associations going from pathogenic to beneficial
161 through neutral [34,35] (**Figure 1**) as revealed by more and more sophisticated methods (see
162 for instance Mercado-Blanco, 2018 [3] and **Outstanding question 1**). The microbiota
163 corresponds to all microbes associated with a plant and the pool of microbial genes
164 corresponds to the **microbiome** [4,36]. In addition, it appears that (i) from one individual to
165 another the microbiota and the microbiome are different, (ii) within the same individual,
166 several microbiomes or microbiota co-exist among different tissues [37,38] and (iii) microbes
167 might support various plant functions. Therefore, to investigate a potential link between the
168 microbiota or microbiome and declines, it is necessary to (i) analyze the diversity of
169 associated microbes, (ii) determine how microbes interact amongst themselves and with the
170 plant and (iii) highlight their respective potential functions and their impact on WP
171 metabolism and development.
172 The short and long-term interactions between host-microbe and microbe-microbe
173 mediate both host and microbial properties and are essential for the health of the host
174 [3,34,39]. Plant microbiota is carried out either by vertical transmission through the seeds or
175 by horizontal transmission through environmental sources [40]. Within plant microbiota,
176 beneficial microbes (i) provide or extend major metabolic functions of plants, especially in
177 terms of nutrient acquisition [3,41,42], (ii) promote plant resistance against biotic and
178 abiotic stresses [43,44], (iii) mediate metabolites production and (iv) support seed
179 germination [45]. Considering the importance of the gained functions, some authors account
180 microbiome for a 'second plant genome'. Combination of plant host and microbiota is thus
181 referred to as 'holobiont' (**Figure 1**), which can be defined as 'the genomic reflection of the
182 complex network of symbiotic interactions that link an individual of a given taxon with its
183 associated microbiome' [42,46,47]. The holobiont concept applied to plants allows a new
184 interpretation of the **facilitation** concept in plant ecology, the microbiota being considered
185 as a 'facilitator' element providing additional functions to the holobiont and adjusting to
186 environmental conditions that are optimal for survival and to keep or reinforce plant
187 **homeostasis** [48]**.**
188

189 The **hologenome** theory takes the holobiont as a unit of selection in evolution [49],
190 where the microbiome is associated with the plant genome both evolving in parallel. Pioneer
191 descriptions of plant microbiota have been published for model plants such as *Arabidopsis*
192 *thaliana, Medicago truncatula* and *Lotus japonicus* [50–52]. Microbiota of WPs has been
193 described on poplar [53–55], oak [56,57] and grapevine [5], either on a plant compartment,
194 including root system [34], trunk [58], **phyllosphere** [55], fruits [59], or as a comprehensive
195 analysis [54,60].
196
197 *Concept of '**core microbiota'**: any bacterial or fungal species shared in healthy and diseased*
198 *plants*
199 Plant diseases, either physiological or ecological, are often associated with changes
200 or compositional deviations from a 'core microbiota' of the holobiont [50] (**Figure 2)**. The
201 core microbiota concept emerged with the discovery that plant microbiota differs from
202 rhizospheric microbiota. Briefly, healthy plants favor colonization by commensal microbes
203 and avoid its colonization by pathogens [3,50]. The core microbiota varies with plant age and
204 compartment as well as soil properties [61,62]. The idea of a 'functional core microbiota'
205 playing a central role in plant physiology and health is now admitted [63], and is often
206 described as the sum of 'the good' (plant beneficial microbes), the 'bad' (plant pathogenic
207 microbes) and 'the ugly' (human pathogenic microbes) [35]. From one plant to another, core
208 microbiota does not consist of identical microbial taxa, but rather different taxa that ensure
209 the same set of essential functions for the holobiont fitness [63]. **Key or hub species** of this
210 core microbiota can be affected during the onset of declines, making the holobiont
211 ineffective against the spread of symptoms.
212
213 *The holobiont functioning: exchange of good practices between partners?*
214 ***A chemical and molecular dialogue within holobiont.*** Within the holobiont, plant-microbe
215 and microbe-microbe communicate mainly through chemical and molecular signaling [64]. A
216 large part of microbiome studies focused on the **rhizosphere** were dedicated to quorum
217 sensing (strictly microbe-microbe communication) and signaling molecules [65] such as
218 volatile organic compounds, phytohormones or antimicrobial peptides [66]. Different
219 communication tools are used to recruit beneficial microbes, to activate desirable microbe
220 traits, induce systemic defense, coordinate microbial population behavior and activity, shape

221 rhizomicrobiome or establish mutualistic symbiosis with fungi or bacteria [66]. For instance,
222 mycorrhizal fungi form mutualistic associations called **mycorrhizas** [57,67–70], able to
223 transfer signaling molecules and nutrients between plants through **common mycorrhizal**
224 **networks** [71] (**Box 4**). Disruption of this communication tools could be linked to the
225 evolution of declines in WP (see **Outstanding question 2**).
226
227 ***Around the roots: a top exchange zone.*** The rhizosphere and the mycorrhizosphere refer to
228 the zone of influence created by roots alone or with the mycelium of mycorrhizal fungi,
229 influencing the composition and function of its microbiota through their exudates, and *vice*
230 *versa* [71,72]. The soil is subjected to numerous abiotic and biotic stresses, affecting the
231 diversity, abundance and activity of living organisms in the soil and consequently the
232 functioning of the ecosystem [73]. Soil microbial community can affect plant survival, growth
233 and tolerance to biotic and abiotic stresses and induce systemic resistance against pests and
234 pathogens both in leaves and roots [34,74,75]. The microbial lifestyle could switch from
235 rhizospheric to mycorrhizospheric or from epiphytic to endophytic depending on
236 environmental factors [76].
237 C and N are the main fuels for plant development and the basis of **rhizodeposition** by
238 root exudation of primary metabolites. Rhizodeposition describes the C-root loss from
239 plants, ranging from 10 to 40 % of assimilated C [77]. The flux of root-derived C (sugars,
240 sugar alcohols, amino acids and phenolics) constitutes a substantial nutrient release in soils,
241 with sugars the main C source for microbes as mycorrhizal fungi and bacteria [78,79]. It was
242 suggested that the more C translocated from leaves to roots, the more C ought to be exuded
243 from roots (*e.g.* [80]) and that C exudation by roots is controlled by factors drawing C into
244 the rhizosphere, such as root colonization by fungi (*e.g.* [81]). In addition to sugars, released
245 amino acids are used by microbial communities as C-N source, but are also recognized by
246 microbial chemoreceptors involved in the early root colonization [82]. Several authors have
247 proposed that differences in sugars and amino acids concentration between root cells and
248 root vicinity mediate root exudation [83], but mechanisms and transport systems remain
249 largely unknown.
250
251 *C-N pools, WP declines and associated microbes: a vicious circle?*

WP storage is highly sensitive to variations in environmental factors. Pathogens involved in declines accentuate some of these physiological dysfunctions in C-N production and flow. In several WP declines, physiological functions needed to assure proper storage are disrupted, although such disruptions might be associated with other type of diseases. For example, in the olive tree CoDiRO disease **(Box 1)**, leaves are subjected to chlorosis or wilting, leading to the reduction of the leaf surface area and a lower photosynthesis rate. In Eutypa dieback or Esca disease in grapevine [84], anatomical analyses have shown a degradation of the photosynthetic systems (*e.g.* chloroplast alteration, thylakoid and endomembrane deformation). In addition, leaf degradation leads to a reduction of stomatal conductance, gas exchanges between atmosphere and the plant, and hydraulic lift from the soil to the leaves [84].

C and N storage can also be reduced after vascular system degradation or plug-blocking. Cankers in the trunk disturb water flux by degrading xylem vessels. The bacterium *Xylella fastidiosa*, involved in Pierce disease and CoDiRO, forms plugs and blocks xylem sap circulation [85]. In the case of horse chestnut bleeding canker, presence of *Pseudomonas syringae* is related to the stopping of water flow through the trunk [13]. In grapevine, *in vitro* tests showed disappearance of all starch reserves after 18 months of *Eutypa lata* activity [86]. Following the damage, three allocations for the non-structural sugars are possible: (i) storage for re-growth when the threat has passed (*i.e.* poplar; [87]), (ii) growth of sink tissues such as fine roots or young leaves, and (iii) synthesis of defensive compounds (poplar: [88]; *Quercus ilex*: [89]). Similar reactions following the damage were recorded for N allocation on common milkweed and red oak [90,91]. N deprivation in the previous autumn (N blocked in roots and woods) leads to budburst disturbance, C resource depletion and tree decline in spring. Finally, root architecture could be modified leading to the reduction of water and N uptake [92].

Finally, the question of which came first, the physiological or ecological disease, is still open (Figure 3). Is it possible that a monofactorial disease, readily identifiable, leads to a weakening of the WP? This would make the affected WP more susceptible to other stresses leading to an overall decline. Conversely, it can be assumed that multiple stresses applied to a WP weaken it, lowering its innate immune response when a specific pathogen arrives, acting like an opportunist (**Box 2**).

283 This question is still open depending on the type of pathogen involved and the type of stress
284 applied. Indeed, a strict biotrophic agent can be disadvantaged during the infection of a
285 plant already stressed and deficient, which cannot provide the necessary nutrients for its
286 metabolism. On the contrary, saprophytes (*e.g.* the GTD responsible fungi) will be favored
287 within already weakened plants. These saprophytic pathogens are often latent members of
288 the plant holobiont, but their virulence would only be expressed during a modification of the
289 microbial community due to the previous weakening of the plant (with for example an
290 exclusion of beneficial endophytes when the carbon status of the plant no longer allows the
291 survival of these).
292
293 Nevertheless, we know that imbalances of microbiota are observed in many declines
294 (**Boxes 2 & 3**). In Acute Oak Decline, comparison between diseased and healthy trees
295 revealed microbiota modifications, with a predominance of *Brenneria goodwinii, Rahnella*
296 *victoriana* and *Gibbsiella quercinecans* in diseased tissues ([57,67–70]. In silver fir dieback,
297 the link between modifications of the microbiota and the presence of disease is not clearly
298 established, even if tree decline has an impact on soil microbiota composition [93]. Decline
299 of photosynthesis rate leads to modify roots and mycorrhizal exudation, changing bacterial
300 growth and community composition as well as nitrification process in and near
301 the rhizosphere and mycorrhizosphere [94–96].
302

303 **Engineering the microbiota, a realistic perspective to cure WPs from declines?**

304 Plant microbiota protect the plant against pathogens *via* direct (production of
305 bacterial toxins) or indirect effect (stimulation of the host immune response and
306 competition for ecological niches) [13,36,39]. Cultural practices are known to impact the
307 composition of WP associated microbiota [97–99]. Therefore, adjusting these practices
308 might be a straightforward option to reduce, prevent or even cure declines [3].
309 The development of agroecological practices, based on the valorization of ecosystem
310 services and of natural biological regulations, responds to a strong societal demand [100]. In
311 this context, beneficial microbes promoting the growth, nutrition and health of plants
312 constitute the basis for a model of functional community useful in the development of
313 agroecological practices [101]. The majority of the results on these approaches come from
314 crops, mostly annual plants like rice, tobacco, tomato, maize or potato (for review, see

315 Compant et al., 2019 [102]). Transferring this knowledge for WP management, requires
316 specific adaptation to perennial plants:

317 ▪ *Development of new rootstock-graft assemblies and ungrafted plants*: having a better
318 tolerance to diseases using beneficial synthetic communities within the selection
319 process. It is tempting to hypothesize that better ecosystem services might be explained
320 by roots and rootstock capacity to associate with different microbiota [103]. The
321 physiological aspects of the rootstock-graft interactions may affect the physiology of the
322 plant and it is possible to optimize the assembly between the two vegetative parts [104–
323 106]. In addition, WP habitat can be also dependent on the local microbiome and
324 especially on symbiotic organisms [107].

325 ▪ *Association of tree species with beneficial microbiota*: sharing the benefits of the
326 microbiota from one individual to another can be considered directly by pooling the
327 microbiota in the soil (especially thanks to the mycorrhizae, see **Box 4**) or indirectly by
328 chemical communication between microorganisms. After identification of the
329 microbiota associated with a tree species and the functional benefits associated with it
330 (*i.e.* root growth promotion), it will be possible to select species and associate them with
331 others for a "microbial complementarity".

332

333 *Conserving microbial functions, an important issue for microbiota engineering*

334 Plant-associated microbiota is a key factor to buffer the effects of biotic and abiotic
335 constraints [65]. However, the description of the taxonomic composition of plant microbiota
336 remains incomplete with the usual and current molecular tools and the processes regulating
337 their assembly need to be further studied [108]. The understanding of the assembly of the
338 microbiota is a research theme of fundamental importance to understand the phenomena of
339 facilitation and rapid adaptation of plants to local environmental constraints. In this line of
340 research, Lapsansky and collaborators [109] proposed the concept of "soil memory" : from
341 one plant generation to another, a given soil would hold its associated rhizospheric and
342 edaphic microbiota. The fitness of perennial plants of the n+1 generation (or of a new woody
343 plant set up in a plot replanting context) would thus be improved, taking advantage of the
344 pre-existing beneficial microbes for their development [109]. Time scales are often
345 considered on an annual or biannual basis for agronomic plants with a short life cycle, but

346 this concept can also be applied to the time scales necessary for the renewal of a forest, a
347 vineyard or at least an orchard. The concept of soil memory could be exploited artificially for
348 example by sampling a given well-balanced forest soil microbiota, multiply it in controlled
349 conditions, before introducing it into nursery greenhouses in plantlets soil.
350
351 *Acting directly on the microbiota composition by microbial inoculation*
352 Some bacteria, endophytic and mycorrhizal fungi can be used as microbial inoculants,
353 owing to their functional properties of antibiosis, lysis, competition or nutrient acquisition,
354 induced resistance or hormonal stimulation. Their functions depend on both abiotic and
355 biotic context [110]. With an annual growth rate of about 10 %, the economic market of
356 microbial inoculants increases rapidly [111]. Although field results on annual crops
357 compared to market gardening are often disappointing compared to promising advances
358 under controlled conditions, we can already try to modify root microbiota of woody species
359 such as oak for Acute Oak Decline [56]. For example, the beneficial role of *Fraxinus ornus*
360 fungal endophytic microbiota against ash decline was suggested, although results need to be
361 further supported [112].
362 Microbial inoculation (see **Outstanding question 3**) could be achieved:
363 ▪ in nursery by inoculating a single or a cocktail of microbial strains by selecting of native
364 or locally adapted inoculants (considering both biotic and abiotic context) or strains
365 with a marketing authorization [113]
366 ▪ on established or mature WP by direct addition of bacterial strains or cocktails of
367 strains by spraying (rather for endophytes) or by reintroduction of mycelial strains as
368 spores or mycelium directly in the soil (*i.e.* mycorrhizal fungi, [114]). Such additions
369 could be repeated until the microbial imbalance ends.
370 ▪ by indirect regular supplementation by complantation (*i.e* replacing dead plants, a
371 cultural practice largely used in vineyards) or by using plant cover as a reservoir of
372 diversity [115].

373 A key issue is that the introduction of beneficial microbes into an established
374 holobiont is not easy to sustain over time. The microbial populations introduced by humans
375 can decrease over time and thus their beneficial effects disappear. They can also eliminate
376 native beneficial microbial species, changing the functional balance of the ecosystem.

377 Nursery manipulations (early stages of plant development) would reduce the odds of
378 disturbing an established microbial equilibrium [109]. Additionally, it can be difficult to
379 switch from an 'unbalanced microbiota state' to a 'healthy microbiota state', without coming
380 back to the original microbial communities because of the resilience of the system, which
381 would make it difficult to keep the new equilibrium over time [116]. Additionally, when
382 microbial strains are characterized as beneficial for plants, the question of the specificity of
383 certain strains for targeted cultivars will prevail. Results from lab experiments may be
384 difficult to implement in the field [39]. Finally, it becomes clearly necessary to include
385 microbiota in plant breeding strategies and in the analysis of varieties and rootstocks
386 performance to limit the loss of microbial genetic diversity, inherent in current agricultural
387 systems and practices.
388
389 *Acting indirectly on the microbiota composition: impact of agricultural practices*.
390 Some agricultural methods are specific of WPs agro-management and might act indirectly on
391 microbiota composition. For example, yearly dead parts of woody plants are often removed
392 because they are thought to contain detrimental microorganisms. However, they represent
393 a valuable carbon source and their removal would contribute to the reduction of organic
394 compounds within the soil which in turn affect soil microbiome [117,118]. If the risks of
395 contamination are too high for some declines and prevent application of grinding dead
396 wood, another option might be to spread dead parts after complete or partial combustion.
397
398 Grafting is a technique widely used within WPs, such as grapevine, olive and citrus
399 trees [73]. Some cultivars or rootstocks as well as clones are more tolerant to pathogens or
400 are physiologically different: the nature of the host influences the susceptibility to a disease
401 (*e.g.* GTDs in grapevine [119]), an apoplectic disorder or a physiological disturbance (*e.g.* the
402 decline of the grapevine associated with the use of the rootstock 161-49C, see **Box 1**)
403 [120,121]. As for GTDs, some olive tree cultivars are more susceptible to CoDiRO than
404 others. For example, cultivar 'Leccino' seems to be more resistant [122]. For the grapevine
405 Syrah decline, it has been shown that even if all rootstocks are concerned, 110R and 99R are
406 more sensitive than others, so their use is not recommended. A very strong clone effect was
407 also observed [123]. These differences in susceptibility could be related to differences in
408 associated microbiota. Rhizodeposition, which is related to the recruitment of rhizospheric

microbes, has been shown to depend on the genotype of the rootstock in apple trees [124]. Within other plant compartments, an influence of the rootstock-scion combination genotype and of WP genotype on microbial diversity is also suggested (*e.g.* the endophytic microbiota in apple trees [125], the bacterial endophytes in olive trees [126], the rhizospheric microbiota in grapevine [127] or the arbuscular mycorrhizal community in citrus [128].

It has been shown that the diversity of organisms (plants, animals and microbes) is positively affected in organically managed or low-farming systems, compared to systems under integrated management [102]. Soil diversity has been studied, particularly in vineyards, where a link was found between soils under green manure and highest soil microbiota diversity, compared to other organic or biodynamic agro-management practices [129].

Finally, since microbiota associated with plants can vary from one species to another, and even from one individual to another within the same species, strategies of association of different species within the same agricultural system can be considered [130]. Thus, a plant could take advantage of the beneficial effects of the microbiota of the neighboring plant, in particular the rhizospheric microbiota, and *vice versa* (see **Outstanding questions 4 and 5**).

Concluding remarks and future perspectives

Improving longevity of WPs is a major challenge considering their declines. A major feature would be to understand, not only the physiology and the ecology of WPs, but also of their holobionts. Microbiota and by extension the microbiome could offer new engineering solutions to prevent and even cure WP declines only if (i) we take into account the specific physiology of WPs, especially fluxes of C, N and water between sources and sinks that are changing over seasons and years and (ii) the chemical and molecular dialogues between microbes and between the WP and microbes. Keeping the homeostasis of WP holobiont would necessitate to carefully balance its resources between growth, storage, reproduction and defense. From nursery to fruit and berry plantations, considering the use of microbiota portfolio adapted to specific conditions (*i.e.* climatic, chemical and biological stresses) will constitute a major step towards a better understanding and management of the agro-ecological outcome of WPs holobionts (see **Outstanding questions**).

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Text Boxes

Box 1. WP declines and consequences on the productivity of fruits

The question of which came first, the pathological or physiological disorder, is difficult to answer. Most of the time, WPs are considered as asymptomatic as no visual declines are observed and some plant compartments (*i.e.* vessels, roots) are difficult to access. So, WP weakening is already under way when the first symptoms of the disease or decline appear. In addition, there is a bias on several species since we are more focused on plants producing wood, fibers, berries and fruits for human nutrition. Grapevine (*Vitis vinifera* L.) and olive trees (*Olea europaea* L.) are worldwide distributed crops of significant economic importance and are currently facing several diseases, due to physiological imbalance of WP tissues and to fungal or bacterial agents. The rootstock 161-49C in grapevine develops limited C storage and displays disturbance in xylem (*i.e.* thylose) and phloem (*i.e.* smaller diameter) leading up to 50% of unproductive vineyard [121]. The main declines affecting mature grapevine plants are grapevine trunk diseases (GTDs) caused by several fungal species [86,131]. GTDs are currently affecting vineyards throughout the world. Approximately 13 % and 14% of respectively the French and Californian vineyards are unproductive. The Olive Quick Decline Syndrome (or CoDiRO, for Complesso del disseccamento rapido dell'olivo), whose symptoms look like those of grapevine declines, is mainly caused by the bacterium *Xylella fastidiosa*. CoDiRO, originally detected in the olive groves of Salento in Italy in the late 2000s, is

778 expected to expend to the rest of the Mediterranean basin and California [132]. Worldwide
779 olive production has recently decreased by about 25% and in Italy by 50%.
780
781 **Box 2. Link between WP declines, pathogens and holobiont imbalance**
782 It seems that pathogenic agents (fungal, bacterial or viral) can trigger diseases on healthy
783 trees acting as "primary factors" when using biotic diffusion vectors or as "secondary
784 factors" when the pathogen benefits from the weakening of the tree (*e.g.* another disease,
785 pruning wounds). This weakening can result from significant climatic (*i.e.* drought, extreme
786 fluctuation in weather conditions), chemical (*i.e.* excessive fertilizers) and biological stresses
787 (*i.e.* insects), poor plant selection for the location, physical constraints, improper planting
788 practices, poor soil conditions and physical injury. It is likely that a given disease is not
789 always related to the presence of a particular pathogen alone, but would result from a
790 combination of adverse factors and the presence of one or several pathogens. In addition,
791 external factors are necessary to influence the transition from an endophytic to a pathogenic
792 state of some fungi in asymptomatic tissues state [133]. The intensity of the disease related
793 to pathogen leads to the modification of the holobiont and depends on either the WP (*i.e.*
794 cultivar) or the balance of microbes (*i.e.* epiphytic and endophytic microbiota) [134].
795
796 **Box 3. Are some microbial species always present in the microbiota of woody plants**
797 **exhibiting different declines related to pathogens?**
798 The same pathogenic species are often involved in declines affecting various WPs and act as
799 opportunists. Similar fungal species from the *Botryosphaeriaceae* (endophytes, saprophytes
800 and some pathogenic) are associated with many declines [135] and found in GTDs, Coast
801 Redwood Trees Decline [136,137] and Branch Dieback of olive [138,139]. More than 300
802 species of plants are susceptible to *Xylella fastidiosa* in the world [85,140] and some strains
803 carried by xylem-sap feeding insects (*e.g.* leafhoppers and spittlebugs), cause fatal diseases
804 in grapevine (Pierce disease), olive and citrus trees. The bacterium *Pseudomonas syringae*
805 infect orchards (*e.g.* cherry, pear, plum and apricot) weakened by water stress or injury and
806 are involved in horse chestnut bleeding canker [13,141].
807
808 **Box 4. Common mycorrhizal networks: a role of sentinel in prevention of decline?**

809 Plant–plant interactions (*e.g.* facilitation, competition) are among the fundamental
810 processes that shape structure and functioning of plant communities. Within the fungal
811 component of the root microbiota, mycorrhizal fungi form mutualistic symbiotic associations
812 called **mycorrhizas** [142]**.** Around 90 % of terrestrial plant species including fruit and olive
813 trees, grapevine and tree species cultivated for their wood are mycorrhized. Mycorrhizal
814 fungi are able to form **common mycorrhizal networks (CMN)** linking roots from the same or
815 different species. CMNs benefit to host plant in many ways, including plant-plant facilitation
816 or nutrition [3]. Since the highlighting of intra-kingdom communication between plants and
817 microbes, especially between plants and bacteria, it has been shown that molecules other
818 than nutrients can pass between microbes and their host plant. Bidirectional nutrient
819 transfers of carbon (C) between ectomycorrhizal tree species such as birch and Douglas fir
820 [143] and nutrient exchanges between endomycorrhizal plants [71] have been shown. We
821 thus define a CMN formed by ecto- or endo-mycorrhizal fungi that link plants together.
822 Transfer of different molecules may be bidirectional between plants and CMN can improve
823 interplant nutrition and growth through plant-plant facilitation. CMNs can also induce plant
824 defense responses and plant communication through phytohormones (*e.g.* jasmonic acid,
825 methyl jasmonate, zeatin riboside) and therefore have a strong potential as a biocontrol
826 agent. The role of arbuscular mycorrhizal fungi as potential bridge between different plants
827 in the spread of a disease has recently been hypothesized, for example with Potato virus Y or
828 following a necrotrophic fungus attack [144]. Indeed, in addition to the competitive role of
829 arbuscular mycorrhizal fungi against pathogens by **allelopathy**, CMN can act as a conduit
830 carrying chemical signaling compounds emitted by the attacked plant. These links make it
831 possible for a plant to send warning signals during an insect or pathogenic attack to the
832 network of plants connected by the CMN 'informing them' of the attack. In this context, an
833 interesting perspective would be to study how this CMN would transfer the information of a
834 pathogen attack for a 'sentinel' plant to a neighboring plant, which could preventively
835 activate their defense mechanisms and enhance their immunity.
836
837 **Figure legends**
838 **Figure 1. The woody plant holobiont.**
839 It is essential to consider the woody plant (WP) as a "holobiont", *e.g.* the tree and its
840 microbial continuum from soil to leaves. The microbiota resides on (epiphytic microbiota) or

841 within (endophytic microbiota in the phyllosphere, the lignosphere and the rhizosphere) any
842 of a number of WP tissues. Interactions exist between the WP and its associated microbes,
843 and among microbes. These microbes can be beneficial (*e.g.* better fitness, nutrition,
844 immune defense), pathogenic (*e.g.* diseases) or neutral for the WP.
845
846 **Figure 2. Woody plant declines: a role of the microbiota**
847 The woody plant (WP)-associated microbiota is made up of bacteria, fungi, viruses, protists,
848 archae and oomycetes. The microbiota could either enrich or weaken some physiological
849 functions of the WP. We hypothesize that the taxonomic composition and functions of the
850 WP-associated microbiota can influence the WP physiological status. The plant stays healthy
851 with a given balance of microbiota. On the contrary, an imbalance of microbiota (as cause or
852 consequence of the decline), leads to visible symptoms, whose origin can be physiological,
853 cultural and pathological. Various options may be used to cure some WP declines: a direct
854 inoculation of specific microbial species (*e.g.* involved in phosphorus mobilization) in order
855 to restore the balance, or by providing specific microbial species with targeted nutrients to
856 promote their growth.
857 In this figure, pie charts only reflect the distribution of the microbiota and the microbiome.
858 We have chosen some genes, not an exhaustive list, encoding proteins involved in functions
859 of WP metabolism. Similarly, a balanced microbiota may correspond to different proportions
860 of microorganisms belonging to each taxon. Taxonomic diversity does not necessarily mirror
861 the functional diversity.
862
863
864 **Figure 3. Tag cloud of physiological and ecological diseases related to woody plant declines**
865 Woody plant (WP) declines have multi-factorial determinants (*e.g.* cultural practices,
866 parasites, abiotic stresses) and their importance is not clearly established, and may depend
867 on the WP species. This tag cloud (built using https://nuagedemots.co/) depicts factors and
868 keywords commonly mentioned on WP declines in references used in this review, without
869 any causal relationships. In WP declines, it would appear that microbiota could be a reliable
870 indicator.
871
872 **Glossary**

873

874 **Allelopathy:** the chemical (excretory products, metabolites) inhibition or regulation of one
875 organism by another.

876

877 **Common mycorrhizal network**: A continuum network formed by both endo- and
878 ectomycorrhizal fungi connecting plants with each other *via* their mycelium. Common
879 mycorrhizal network allows exchanges of nutrients and other chemical substances between
880 connected plants.

881

882 **Core microbiota**: All microbial species (bacteria, fungi, viruses, protists) which predominate
883 at surface or inside a living organism (here plants). Plant core microbiota could be defined by
884 a set of microbial species always found in plant of different genus.

885

886 **Core microbiome**: Set of essential functions provided by the microbiota of a plant found
887 from one plant to another.

888

889 **Decline**: Gradual reduction of growth, vigor and productivity in a woody plant due to
890 multiple abiotic (water or thermic stresses...) and biotic stresses (pathogens, insects…) and
891 likely to an unbalanced microbiota.

892

893 **Dieback**: Progressive death of twigs and branches which generally starts at the tips.

894

895 **Endophyte**: Microorganism (mostly bacteria or fungi) that lives inside tissues of other
896 organisms, in a symbiotic way, with beneficial effects or at least with no negative
897 consequences for the host fitness. Microorganisms involved can therefore be commensal or
898 beneficial, but they can also be saprobes or latent pathogens.

899

900 **Endosphere**: Internal regions of plant tissues that can be colonized by microorganisms.

901

902 **Epiphyte**: Microorganism (mostly bacteria or fungi) that lives on the surface of a given
903 organism.

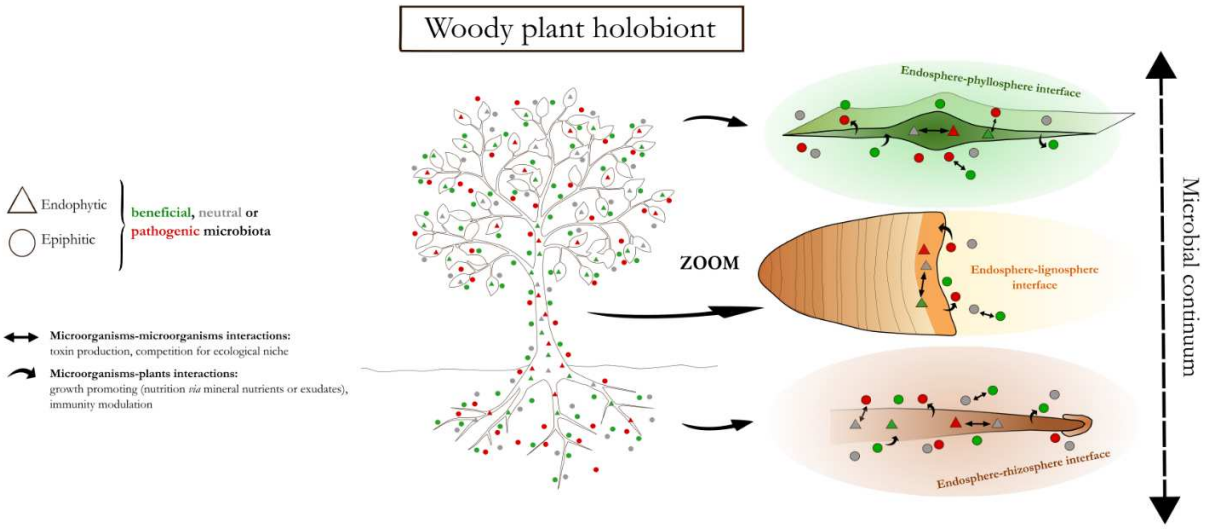
904

905 **Facilitation:** A positive interaction that can contribute to assembling ecological communities
906 and preserving global biodiversity.
907
908 **Holobiont**: Sum of the different species that forms an ecological unit. Here, we limit our
909 definition to the plant and all its symbiotic microbiota.
910
911 **Hologenome**: The host and microbiome genomes. The host genome is highly conserved with
912 slow genetic changes. The microbiome genome is dynamic (*e.g.* horizontal gene transfer,
913 mutation) and can change rapidly by modifying microbial populations in response to
914 environmental changes.
915
916 **Homeostasis**: The maintenance of a relatively steady state or equilibrium in a biological
917 system by intrinsic regulatory mechanisms.
918
919 **Key or hub species**: A small number of taxa that are strongly interconnected and having a
920 severe effect on communities.
921
922 **Lignosphere**: Botanically, it is the micro-ecosystem of the trunk and branches surface,
923 considered as a possible habitat for microbes.
924
925 **Microbiome**: Set of genes brought by microbes forming the microbiota within a holobiont.
926
927 **Microbiota**: Community of microbes associated with the plant (bacteria, archaea, fungi,
928 viruses, protists and other microeukaryota).
929
930 **Mycorrhiza**: From *mukes*, fungus; and *rhiza*, root. Intimate association between roots from
931 90% of land plants and specialized soil fungi. At least seven types of mycorrhiza exist, but
932 ectomycorrhiza and arbuscular mycorrhiza are the most common.
933
934 **Phyllosphere**: Botanically, it is the micro-ecosystem of the leaf surface, considered as a
935 possible habitat for microbes.
936

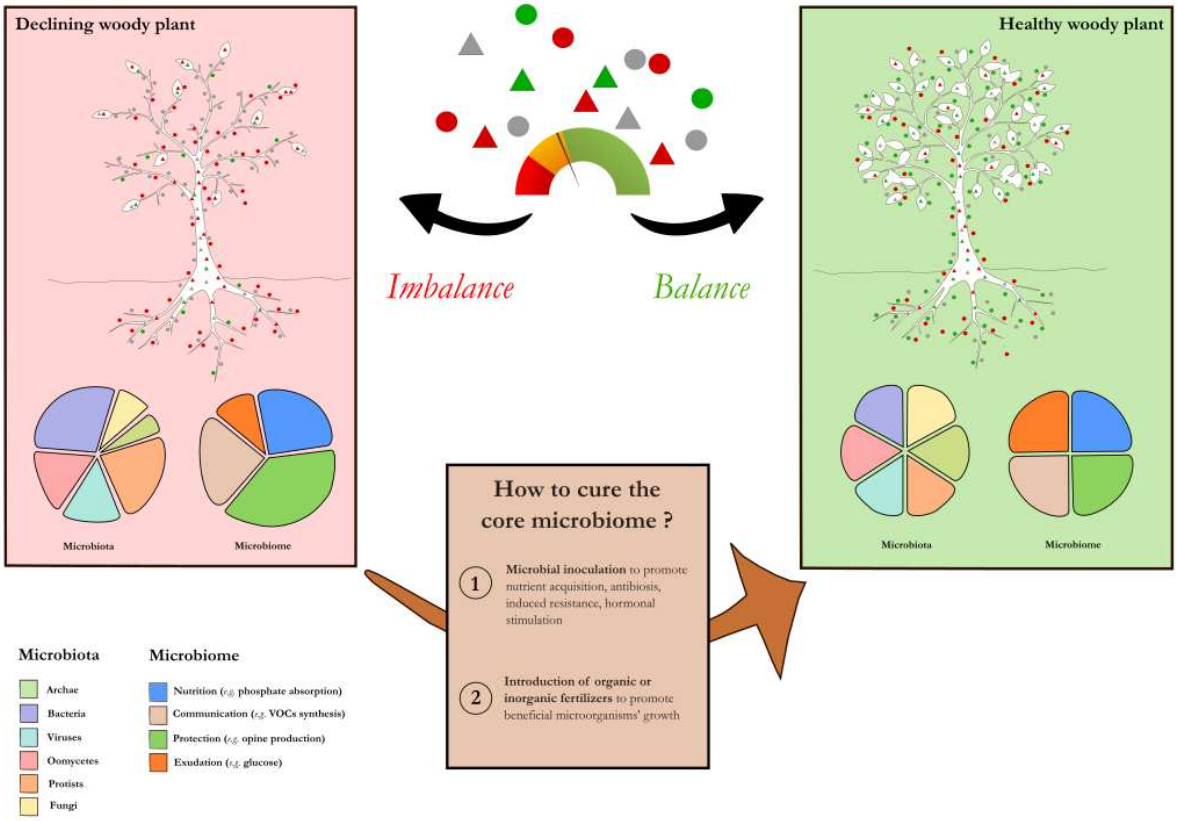
Rhizosphere: Volume of soil surrounding living plant roots that is influenced by root activity and hosting specific rhizospheric microbes.

Rhizodeposition: The release of materials from plant roots into the rhizosphere, including soluble and insoluble exudates, lysates and gases.

Symbiont: Organism establishing a close and long-term interaction with its host (here the plant).


Woody plant holobiont
Endophytic
Epiphitic
beneficial, neutral or pathogenic microbiota
Microorganisms-microorganisms interactions:
toxin production, competition for ecological niche
Microorganisms-plants interactions:
growth promoting (nutrition via mineral nutrients or exudates), immunity modulation
ZOOM
Endosphere-phyllosphere interface
Endosphere-lignosphere interface
Endosphere-rhizosphere interface
Microbial continuum

Woody plant declines: A role of the microbiota ?



Endophyte
Hologenome
Opportunists
Abiotic
Interaction
Weakened
Reserves
Toxins
Susceptibility
Root
Pool
Shoot
Trunk
Death
Viciouscircle
Microbiota
Biotic
Carbon
Practices
Bacteria
Virus
Grafts
Epiphyte
Fungi
Nitrogen
Dysbiosis
Decline
Network
Soil
Tolerance
Pathogen
Climate
Symbiosis
Functional
Varieties
Woodyplant
Stress
Immunity
Flux
Diversity
Healthy
Physiology
Microbiome
Holobiont
Hubspecies
Symptoms
Biocontrol
Agroecology
Mycorrhiza