MOTHER TREES, ALTRUISTIC FUNGI, AND THE PERILS OF PLANT PERSONIFICATION

La grandeur de l'homme est grande en ce qu'il se connaît misérable. Un arbre ne se connaît pas misérable.

The greatness of man is great in that he knows himself to be miserable. A tree does not know itself to be miserable.

Blaise Pascal, Pensées (1670; # 397)

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A recent article in the New York Times [1] has drawn attention to the growing doubts about the true role of the common mycorrhizal networks (CMN or WWW, wood wide web) connecting the roots of trees in forests. In particular, the claim of a substantial carbon transfer from “mother trees” to their offspring and nearby seedlings through the CMN is being questioned. Recent reviews show that evidence for the Mother Tree concept is inconclusive or absent. Moreover, this concept contradicts numerous well-known observations on development patterns of regrowth in forests. The origin of the Mother Tree Concept seems to stem from a desire to humanize plant life. This may appeal to many people, but such anthropomorphic perspective and vocabulary can lead to misunderstandings and false interpretations and may eventually harm rather than help the commendable cause of preserving forests. Two recent books serve as examples: “The Hidden Life of Trees” (2017) by Peter Wohlleben [2], and “Finding the Mother Tree” (2021) by Suzanne Simard [3].

The Hidden Life of Trees: Anthropomorphization and Conjecture, but not Science

Probably the best example of anthropomorphizing plants is the book “The Hidden Life of Trees” [2], which is a best seller with over 35 editions and is available in different languages all over the world. While mentioning the scientific work of Suzanne Simard, but by ignoring extensive scientific findings contradicting his viewpoints, Wohlleben ascribes to plants (in this case trees), a number of human characteristics: feeling pain, being happy and caring for other trees, being able to communicate with other trees, and being capable of creating strategies for the benefit of the group. These are hallmarks of conscious organisms, which plants are definitely not [4, 5]. A striking example is his claim that a forest has no interest in losing “weaker” members of the same species, instead postulating that competition between trees is restricted to interspecific interference, which contradicts fundamental knowledge of forest ecology (see Box 1).

At the end of his book, Wohlleben even goes so far as to propose abolishing the “arbitrary” separation of animals, plants, and fungi. Even the most benevolent critics of his book feel this demand goes too far, blatantly disregarding 300 years of biological research [6]. Consequently, Wohlleben’s book has been severely criticized on

numerous occasions for the misinterpretation and distortion of scientific data [7, 8, 9, 10]. We draw attention to the preface of Halbe's book [7] written by the well-known plant biochemist Nikolaus Amrhein. He states:

"The majority of my colleagues, even if they had read the book at all, hold Wohlleben's ideas so evidently unscientific and untenable, that they did not deem it necessary to criticize it publically". (engl. Translation).

Although several scientists have challenged the claims of Wohlleben, this has had little influence on the responsiveness of the general public to Wohlleben's pseudo-scientific interpretations of plant life. He continues to attract new followers, and has even become a TV personality in Germany. In the meantime, he is also being used by various groups as a key witness for alleged "forest devastation" caused by false forest management and is often seen participating as a forest expert in talk shows. The extent to which his expertise is credible and based on scientific facts is not questioned in these formats where obviously other mostly economic considerations are important. This certainly becomes problematic, when politicians and administrators start to rely on this "expertise", for example, Wohlleben was invited to give an "inspirational speech" at a scientific symposium on forests, biodiversity and climate change organized by the European Commission in February 2020. Wohlleben has also been appointed to the advisory board of the UN Decade of Restoration for his "emotional and unconventional communication of knowledge", a knowledge which is mainly based on belief and assumptions. The unwillingness or lack of ability by the media and decision makers to assess the factual basis of Wohlleben's statements (or the deliberate use for their own purposes) is a great concern to plant and forest scientists and has in part motivated this article.

Searching for the Mother Tree

In her book: "Finding the Mother Tree" [3] the Canadian forest ecologist Suzanne Simard submits that trees communicate their needs and send each other energy and nutrients altruistically via a network of fungal hyphae in the soil, the common mycelial network (CMN) popularly referred to as the wood wide web (WWW). According to this hypothesis, "hub" or "mother trees" are highly connected to nearby seedlings via the CMN and share their excess C and N with them, thereby, increasing seedling survival and growth. In particular, it is claimed that kin-offspring benefit more from this CMN-mediated nutrient transfer than non-kin plants.

Do Simard's published data and interpretations stand up to a critical analysis? Before going into detail, it should be pointed out that the Mother Tree concept is incompatible with many well-known observations on the growth of forest trees. For instance, an early Finnish study demonstrated that belowground competition hampers seedling establishment [11]. This has been confirmed in many studies where mature trees have been shown to suppress growth of seedlings, for example in maple and pine [12, 13, 14]. This finding has a long history of being acknowledged by foresters. For example, almost a century ago Aaltonen [15] reported that mother trees can greatly impair the growth of their offspring. In fact, the absence of regeneration in the immediate vicinity of the "mother tree" is often described as a "plate effect", meaning that belowground competition from mature trees makes it difficult for regenerating seedlings to establish. The finding that canopy trees impede the survival and growth of seedlings has been the basis for timing of removal cuts in shelterwood regeneration systems [16, 17]. In temperate beech forests, trenching, which prevents root competition by mature trees, has been shown to stimulate growth of the regeneration [18], a fact, established 95 years ago [19]. Fabricius [20] concluded that competition for water by overstory trees is decisive for seedling survival and growth when species-specific light requirements are fulfilled. In contrast, the mother tree concept suggests a negative impact on the offspring after trenching i.e., in the absence of carbon supplied via mycorrhizal links. Thus, the mother tree hypothesis is incongruent with observations of seedling regeneration patterns in forests and also with results from experiments where interactions between large trees and seedlings via CMNs has been hindered.

The seminal publication of Simard et al. [21] demonstrated inter-tree net transfer of carbon (C) but the mechanism remained unclear. The claim that C transfer occurred through a common mycorrhizal network (CMN) caused a wave of enthusiasm among forest ecologists and opened up a new field of research. Following these initial findings, numerous experiments were performed to establish the role of CMNs in C transfer and to quantify the amount of C transferred between plants (e.g., [22, 23, 24, 25, 26]. With the notable exception of Klein et al. [24] and Avital et al. [27], these studies conclude that only insignificant amounts of C were transferred to the receiver plant. Serious criticisms regarding the interpretation of the results of the study of Simard et al (21) were made very early [28, 29], arguing that the transfer mechanism had not been unequivocally established and that no advantage for the receiving plant had been

178 demonstrated. Thus, it is often unclear as to whether the transferred carbon actually
179 enters the root tissue of the receiver tree or is simply being retained in the fungal
180 hyphae at the root-fungal interface [28].

181 The concept of a wood-wide web linking trees in a forest by mycorrhizal hyphae is
182 based on isotopic evidence [21]. WWW received an additional boost when new genetic
183 techniques suggested the presence of below-ground links by the same fungal
184 genotype among many distant trees in a stand [30]. Although the spatial “architecture”
185 implies physical links, intactness of the fungal connections and carbon distribution
186 among trees were not demonstrated [30]. Even in studies with remarkable shifts in
187 abundance of the stable isotope ^{13}C (by which transfer was assessed; e.g. [24]), the
188 magnitude of isotopic ratios was close to those which can arise from natural processes
189 in the tree, rendering the estimates of CMN-driven C transfer in natural ecosystems
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193 described by Henriksson et al. [31] the shifts in abundance of the stable isotope ^{13}C
194 (by which transfer was assessed) that were reported by Klein et al. [24] were close to
195 the magnitude of isotopic ratios which can arise from natural processes in the tree,
196 rendering the estimates of CMN-driven C transfer uncertain. For example, release of
197 root exudates, respiration and re-fixation, degradation of litter and incorporation of the
198 13C into amino acids [32] can result in below-ground redistribution of carbon by soil
199 microbes, soil fauna, and precipitation. Thus, the extent of a directed flux from a donor
200 to a receiver is unclear. Avital et al. [27] found C transfer of a similar magnitude
201 between tree species that were assumed to lack mycorrhizal connections. However,
202 some tree species have the ability for dual mycorrhizal colonization, for example poplar
203 can host both AM and EM species. This trait may be more widespread than previously
204 thought [33], thus, permitting in principle linkages between AM and EM hosts.
205 Therefore, the jury is still out on whether CMNs can play a significant role in C
206 translocation under certain conditions or not.

207 Recent reviews have also drawn attention to the inconsistency of results obtained from
208 experiments using different mesh-sizes to include or exclude roots and mycorrhizal
209 connections between seedlings [34, 35]. In such experiments (see [21, 22, 23]), CMN
210 exclusion did not always prevent C transfer among plants, indicating that CMNs are

not essential for C transfer. However, despite the inclusion of caveats by authors [e.g. 22, 27] to acknowledge that alternative transfer pathways could not be excluded, these studies are nevertheless cited as providing evidence for CMN-mediated C transfer [34, 35]. Henriksson et al. [34] therefore conclude “that evidence of a significant net C transfer via common mycelial networks that benefits the recipients is still lacking. Furthermore, the role of fungi as a C pipeline between trees is difficult to reconcile with any adaptive advantages for the fungi”. Moreover, preferential transfer of C to the roots of kin-plants via CMN as claimed by Pickles et al. [36], has not been confirmed. Indeed, facilitation may be greater when the phylogenetic distance between tree species is greater [37]. In their laboratory study Pickles et al. [36] showed that in two of four kin-kin and kin-non-kin pairs a significant ^{13}C signature was detected in the kin-kin but not in the kin-non-kin pairs. However, the amount of translocated carbon was marginal. The amount of translocated carbon between roots in compartments enabling hyphal connections was similar to that in roots in compartments with pores that did not allow fungal connections. Therefore, Pickles et al suggested that root exudates were exchanged between the compartments and likely taken up by mycorrhizae in the separated compartment.

Simard et al. [38] have raised the possibility that organic N could represent C transferred among plants. However, even if C from a donor plant would be used to synthesize organic N in a CMN (mainly glutamine and arginine), any receiver plant (except for mycoheterotrophic plants) would still contribute with C to this CMN, making the net C gain dependent on the exchange rate of organic N to C which may lead to a net loss rather than a net gain of C for the receiving plant.

CMN Function: Alternative Scenarios

If there is little evidence to support an altruistic function of CMN, are there alternative scenarios that could involve CMN-mediated C and nutrient transfer? First of all, we draw attention to mycoheterotrophs, a group of plants that depend fully or partially on mycorrhizal fungi for their nutrition [39, 40]. They acquire C (and N and other nutrients) from the fungi, which in turn receives C from a host plant. As such they represent the best example of C transfer between plants via a CMN. Mycoheterotrophy occurs both in arbuscular and ectomycorrhizal plants and is the norm for orchids in early developmental stages. It is therefore possible that non-mycoheterophic plants may use a similar mechanism to acquire C from a host plant via a CMN. Notably, such a parasitic

mode of seedlings would predict that seedling growth and performance would be enhanced in the vicinity of large trees, a pattern that is opposite to the actual pattern of regeneration observed in forests. As discussed by Henriksson et al. [31], it has been suggested that conifer seedlings in a CMN acquire N in relation to the C delivered to the fungi, indicating competition, rather than sharing, among connected plants. This is in line with studies of arbuscular mycorrhizal interactions as well [41, 42].

Another possibility is that if the same fungus connects with two separate tree individuals via mycorrhizae, the fungus may trade with both these trees for its own benefit. If such trading invokes transport of organic N compounds from the fungus to one of the host trees, and C in organic N molecules was derived from trading N for C from the other tree, then C would arguably be transferred between the tree individuals through a CMN. However, the organic N absorbed by the first tree would be in exchange for C, substantially reducing or nullifying any net C transfer. Thus, as shown above, there are alternative mechanisms explaining how C may move from one individual to another through a CMN.

Public Reception and Criticism of the Mother Tree Concept

As with Wohlleben's book, Simard's book has also become a best seller and has been praised by a number of plant scientists (see https://suzannesimard.com/finding-the-mother-treebook/praise-for-finding-the mothertree/?doing_wp_cron=1679703014.6174020767211914062500 for examples). However, the majority of these reviewers lack experience in mycorrhizal research and from the tone of their reviews are obviously sympathetic to an anthropomorphic viewpoint. Most recently criticism of Simard's Mother Tree concept has been voiced in two major reviews. Whereas Henriksson et al. [34] have questioned the validity of the scientific evidence (see above), Karst et al. [35] have analyzed the citation record of scientific publications investigating CMNs in relation to the Mother Tree concept. They identified a gradual shift over time from more nuanced referencing, where caveats and uncertainties inherent in these studies are mentioned, to a higher frequency of citations where these problems are no longer acknowledged. This has led to a full-blown controversy over the Mother Tree concept (https://www.saltwire.com/halifax/news/sadly-mother-trees-dont-act-like-mothers-and-avatars-tree-of-souls-doesnt-exist-100842634/). Interestingly, one of the coauthors of the Karst et al. [33] review was Melanie Jones who was a coauthor on the 1997 Simard

et al. paper where the WWW concept was originally introduced, and the lead author of this review, Justine Karst, has also published jointly with Suzanne Simard on numerous occasions. This makes this controversy even more highly charged. Recently, and together with Melanie Jones, Karst has also written a critical commentary on Simard's work [43].

In addition, and in response to Simard's continued defense of the Mother Tree concept as given in numerous video presentations, Justine Karst and Jason Hoeksma have found it necessary to give detailed rebuttals to the various claims of Simard in the form of open letters to the responsible TV channels:
https://karstlab.ualberta.ca/wp-content/uploads/sites/47/2023/04/BBC-Trees-talk-to-each-other.pdf
https://karstlab.ualberta.ca/wp-content/uploads/sites/47/2023/04/CBC-trees-talking.pdf talking.pdf

In our opinion, not only are the arguments given by Jones, Karst and Hoeksema convincing, but they reveal that some of the data on which Simard has based her claims are based upon non-peer reviewed theses work performed under her supervision. More disturbing is the fact that, especially in regard to kin-recognition and preference, her claims do not correctly reflect and even contradict the data presented in these theses. This casts great doubt on the scientific credibility of Simard's book. Despite its broad appeal, and although being a fascinating personal account of her life in science, Simard's book lacks a sound scientific basis, and does not even faithfully represent the published forestry and plant science literature.

Publication Policy: Substantiated Facts versus Fiction and Profit

As the experience with the books of Wohlleben and Simard shows, the serious misrepresentations of plant life which now prevail in the popular press might have been avoided if established plant scientists had rapidly responded to the publication of such pseudo-scientific interpretations. But most blame lies with the publishing houses who do not make the effort to determine whether a submitted book manuscript deals with facts or fiction. Publishers assume that fact-checking is a responsibility of the authors, but as we have seen with Wohlleben's book self-regulation does obviously not work. It might help if book publishers used a peer-reviewing system as in scientific journals. But where commercial interests prevail, selling fictional accounts (and this in essence is what the books of Wohlleben and Simard are) to a lay-person audience that is

responsive to anthropomorphic language is good for business. This does not mean that books like those written by Wohlleben and Simard should not appear in print, and publishers should not be allowed to make profits from their sale. But the general public has a right to know what kind of a book they are buying, and the publishers should label them for what they are: factual books or fictional accounts. Unfortunately, the latter promulgate a distorted and false view of the plant and fungal worlds. More precariously, the marketing of books like those of Wohlleben and Simard by the media takes advantage of people's desire for "harmony" und thus influences the public perception of plants making it harder to base relevant policies and decisions on verifiable facts. For example, one could easily imagine that basing management decision on the mother tree concept could result in forests with low vigor regeneration of a limited set of tree species.This may decrease the resilience and adaptive capacity of future forests..

Anthropomorphism and Plants

Anthropomorphic vocabulary not only allows pedagogic analogies, but it can also be used to enhance our emotional connection with animals and plants. Specifically, it leads to a lack of objectivity and to the need to interpret experimental data in the sense of a recognizable universal life template. The non-human specificity of fungi and plants is ignored, a gross oversight given that some of the most basic processes, for example, reproduction, differ greatly among these kingdoms [44, 45]. Nevertheless, the desire to humanize plant life has been the goal of many recently published books. Some blatantly propagate a shamanistic viewpoint, claiming that plants can even speak to one another and to the book's authors (e.g., [46, 47]). Without scientific proof, this is pure mysticism. The other group of writings expresses the viewpoint that plants are intelligent conscious organisms and can not only make decisions (e.g., [48, 49]), but apparently can actively care for each other [3].

Opinions on anthropomorphism in the plant sciences range from complete repudiation: "*Anthropomorphism is taboo in science because it deceives us more often than it helps" (Flinn* [50]*),* to a hearty embrace ("*Yeah, I love it",* Monica Gagliano in interview with Andrea Morris, [51]. However, unlike Gagliano who suggests that this is a new way of thinking about plants, the humanization of plant function has been around since Victorian times (see [52] and references therein), and continues up to the present time in the much disputed concept of Plant Neurobiology (see [53, 54] for a discussion).

Anthropomorphism and its impact on Forest Management and Ecosystem Services

Even in serious newspapers reports are increasingly appearing which question the idea of managing forests for wood production based on the belief that trees are sentient beings [55]. In these cases, the system of clear-cutting and planting is used exclusively as **the** prevailing management scenario while the manifold, well-researched and effectively practiced alternatives to clear-cutting are ignored, even though these alternatives show that forests can be managed in a close to natural way while maintaining their integrity [56, 57, 58]. It remains open whether these omissions are intentional or the result of too superficial research. Both are unacceptable.

The humanization of trees and the description of forest management as a mainly destructive industry serving purely economic interests have several serious effects on the public. First, it suggests that selfless, benevolent organisms with feelings, the trees, are being killed for the sake of a profit-oriented industry. Wohlleben persistently conceals the fact that the renouncement of wood use (which he does not completely exclude, but would like to see drastically restricted) and his hostility to the cultivation of conifers would require either a radical reduction in the use of wood, e.g. in the building sector, or an increase in imports from other parts of the world, or the substitution of wood by other materials such as concrete or steel, which typically require high amounts of fossil energy for their production [59]. However, readers do not learn that these alternatives to the sustainable use of domestic wood have a negative influence on greenhouse gas emissions. Thus, they are oblivious about the environmental costs and likely failure to meet political climate mitigation goals associated with a massive restriction of the use of wood. The hands-off approach to forest management promoted by Wohlleben also ignores that maintaining all the benefits from forests in Central Europe requires in many cases active silvicultural management to adapt them to global change in pace with rapid environmental changes [60]. This necessary restoration and adaption comprise for example changes in tree species composition, the diversification of tree species composition and stand structures, establishment of advance regeneration, and regular stand tending to maintain tree diversity and promote individual tree vigor [61].

There is wide agreement among forest scientists that natural adaptation of most forests, suggested as the only suitable way by Wohlleben and others, would not be

fast enough to avoid massive disturbances and thus severely restricted provision of important ecosystem services. This hands-off approach would therefore risk the development of highly vulnerable instead of resilient and adaptive forests. Spittlehouse and Stewart [62] made this point very clear 20 years ago and stated *"although forest ecosystems will adapt autonomously, their importance to society means that we may wish to influence the direction and timing of this adaptation at some locations. In other cases, society will have to adjust to whatever change brings. Adaptation is not something to be applied only in the future; actions are needed now in anticipation of future conditions".* Wohlleben's and Simard's readers, however, gain the impression that restricting forest management would solve all problems related to forests and that clear-cutting is the only way forestry is practiced. Feasible and proven concepts available to use the renewable resource wood while preserving the integrity and functionality of forest ecosystems, for example by close-to-nature forestry approaches or by managing forests as complex adaptive systems [63], are ignored. It is also widely ignored that forests in densely populated countries mirror the societal demands at the time of their establishment by natural regeneration or plantings with a remarkable time lag. Thus, the composition and structure of today's forests can only be understood against a historical background and is not the result of decisions by a small group of people, the foresters, but by society [64]. If the current societal demands are not met anymore and/or if adaptations are needed due to changed environmental conditions, forest stands need to be adapted and restored (see, for example [65]). This is a long-lasting task under highly uncertain conditions since neither the environmental conditions of the future are known nor the societal demands of future generations. This calls for the creation of forests that could be developed in different directions [66] which require occasional silvicultural interventions.

Another problem associated with the portrayal of trees as victims and the forestry sector as the cause of all problems is that all other non-forestry related impacts on forests such as climate change, atmospheric pollution, eutrophication, introduction of new pests and diseases, fragmentation, land-use change, etc. are ignored. At no stage are readers reminded that it is also their consumption pattern, behavior and mobility that contributes to negative developments of forest health.

Forests have always provided a surface for projection of societal and cultural perceptions and ideas. For example, thoughts about German forests – irrespective of the time-period - essentially ran parallel to the national-political developments of the

19th and 20th centuries [67]. This ranged from the romantic poets and thinkers who sought to root the nation in nature, to the National Socialists who exploited the forest for their ideologies, the production-oriented post-war generation, the turn to close-to-nature forestry in the last three decades, and now to our present-day society which partly views a forest as a social utopia where all trees support each other in harmony. Especially given the future uncertainties, we are most concerned that this kind of thinking will lead to restrictions on active forest management. Limited choices and options will likely leaves us with forests that are ill-adapted and cannot provide essentially needed ecosystem services.

Concluding Remarks

In this article, we have critically assessed the value of two books that have enjoyed enormous success in the popular media. The authors of these two books have used the stylistic device of anthropomorphizing to convey specific ideas that lack supporting evidence to make their message most appealing to the general public. However, as we have demonstrated, although being extremely popular, these books are misleading when viewed as presenting a scientific understanding of forests. They either rely on questionable data interpretations coupled with biased citation selection (Finding the Mother Tree) or lack a solid scientific basis (The Hidden Life of Trees).

So, why chose an anthropomorphic portrayal when this leads to lack of objectivity? In her excellent short opinions paper, Flinn [50] provides us with a clue as to why such dangerous publication strategies have been chosen. We quote: *"In interviews, Simard has said that she purposely uses anthropomorphism and culturally weighted words like "mother … so that people can relate to trees better, because "if we can relate to it, then we're going to care about it more".* Reaching out to the general public to make people care about forests is certainly a praiseworthy goal, but not when it involves the dissemination of a distorted view of the plant world. In other words: the end does not justify the means. We agree entirely with Flinn when she writes: *"… let us seek to understand plants on their own terms. Plants are fundamentally unlike us…*", and with Fortey [6] who states *"Trees are splendid and interesting enough in their own right without being saddled with a panoply of emotions".* In short, anthropomorphism merely clouds the issue at hand. Humanizing plants has not led to any fundamental advantages for scientists studying plant life and has obscured ecological facts. Indeed, spreading the view that forests deserve protection

because they display human qualities could actually harm the cause of conservation, rather than help it.

4463 words

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Box 1: Caring trees and depleted soil carbon – Fiction in The Hidden Life of Trees

Since the information base of Wohlleben's writing is a mix of a few selected paragraphs from scientific articles combined with press releases and websites, one finds few clear factual statements. Yet, some of the cornerstones of his perspective on forests are completely baseless assertions. Two examples are given below:

„I have already mentioned that beeches are capable of friendship and go so far to feed each other- It is obviously not in a forest's best interest to lose its weaker members (p. 15). … "In such a system, it is not possible for the trees to grow too close to each other. Quite the opposite. Huddling together is desirable …" (p. 16)

In fact, it has been known for almost a century [68] that as individual trees grow taller, their demand for space increases and the forest stand approaches a maximum density. This site-carrying capacity depends on the availability of resources and tree species [69]. As even-aged groups of trees grow, intraspecific competition results in a characteristic and mathematically well-described temporal decrease in stem numbers as the size of the remaining individuals increases, the so-called self-thinning rule [70]. This size and density-dependent mortality results in the death of thousands of individuals as closed stands develop from saplings to mature trees. In fact, mortality due to competition is a frequent phenomenon. For example, for European beech it has been shown that competition-related mortality of standing trees is particularly high in young and small trees [71]. Ignoring such facts will lead to dense strands with low vigor trees that are highly susceptible to e.g., beetle attack, drought, fire, wind and snow damage [72, 73, 74, 75], as well as an understory vegetation layer with low diversity and associated lower adaptive capacity to climate change [76]. However, in the social utopia that Wohlleben projects on forests, these small trees are protected and nursed by mature trees.

„For every log you burn in your fire at home, a similar amount of carbon dioxide is being released from the forest floor outside. And so carbon stores in the ground below trees in our latitudes are being depleted as fast as they are being formed" (p 95).

Soil is one of the world's largest C reservoirs. Land-use changes (e.g., conversion of forests to arable land, primary forests to plantations) and intensive forms of forest management (e.g., soil tillage such as ploughing, fertilizing, removal of the forest floor layer, drainage, large-scale clear-cutting, targeted burning of slash and ground

vegetation) can seriously reduce this store. Also, harvesting or thinning procedures at lower intensity can affect soil carbon stocks via changes in biomass input or in microclimatic conditions [77]. There is currently an intensive scientific discourse on this, fueled by the great importance of soil carbon storage in climate change but also by contradictory results from corresponding studies. A recent review shows that, on a global scale, forests' biomass production is closely correlated with soil carbon stocks [78]. However, it is anything but a simple 1:1 correlation (see [79]), as Wohlleben claims in the above quote and interestingly it is the leaf biomass which is correlated with soil carbon stocks not the wood biomass. A decrease in soil carbon storage due to timber harvesting can probably be expected especially where the conditions for soil carbon stabilisation are unfavourable. This seems to be the case, especially on shallow sites in the Alps [80, 81], or where a large part of the organic matter is stored in the humus layer [82]. However, not a single study confirms humus losses as a result of timber harvesting to the extent that Wohlleben claims: "… *a similar amount of carbon dioxide is being released …"*. On average, about as much carbon is stored in the aboveground biomass as in the soil in many temperate forests. This means that if all trees of a stand were harvested, all the soil carbon would be lost. This is not the case because in our latitudes the soil organic matter is stabilised in the soil – a fact well-documented by soil organic matter half-lives in the range of hundreds to thousands of years [83, 84]. Several studies indicate that the humus content in forest soils is not limited by biomass input, but rather due to the capacity of the soil to store organic matter. In case all wood remains in the forest and slowly decomposes as deadwood, soil carbon may increase locally close to deadwood [85], but there are also studies that have found no increase in soil carbon under deadwood [86]. At a larger stand scale, studies that compared soil carbon stocks between managed forest and reserves without wood extraction, have not been able to find systematic differences.

Box 2: Altruistic Fungi?

Many of the claims made by Simard in her book and in video presentations (TED and BBC talks “How trees talk to each other”) are without supporting evidence. Here we list several examples of such instances:

- *Trees send resources to each other through shared fungal networks, and it is claimed that older trees, known as mother trees, use this fungal network to supply shaded seedlings with sugar. (Finding the Mother Tree, pp. 259-278)*

Studying resource transfer between trees is inherently difficult. Alternative pathways to fungal networks must be controlled for and when this has been done, only minute amounts of resources such as carbon and nitrogen have been detected in a receiving plant. Two studies claimed high rates of C transfer from a donor tree to a receiving tree, but it could not be verified that transfer occurred through fungal networks [24, 27]. Other studies, both in the field and in the lab or the greenhouse arrive at fractions of a percent up to a few percent of root carbon in a receiving plant that could have been transported from a donor plant (e.g. [25]).

- *Mother trees recognize their kin seedlings through the CMN. (Finding the Mother Tree, pp.259-278)*

A study by Pickles et al. [36] claims that higher rates of labelled C and N occurred in seedlings that were genetically closely related to the donor plant compared to seedlings more distantly related. But transfer occurred despite separating seedlings with a mesh that would not have allowed for fungal hyphae to connect seedlings. A second study arrived at the opposite conclusion, i.e., higher rates of resources were transferred to more distantly related plants. Also, a Masters’ thesis from Simard’s own laboratory contradicts the claim that mycelial networks may be used by mother trees to send resources preferentially to their kin.
(https://open.library.ubc.ca/soa/clRcle/collections/ubctheses/24/items/1.0103374).

- *Via the CMN, mother trees give seedlings a better chance of survival. (Finding the Mother Tree, pp. 279-303)*

Field observations often contradict the mother tree hypothesis which predicts a higher growth rate of seedlings in the proximity of large trees [33]. In fact, emergence and

growth of seedlings and saplings are in general negatively affected by proximity to large trees [33].

- *Plants use the CMN to transmit messages to one another. This includes chemical signals to elicit wound responses. (Finding the Mother Tree. pp. 279-303)*

There is only one peer-reviewed study suggesting that tree seedlings can send warning signals to each other through the CMN [87]. However, this was a greenhouse experiment, and this signaling ceased when root interactions were allowed to form, as they always do in forests.

- *Dying Trees send their resources to neighboring trees (kin).* (Finding the Mother Tree. pp. 279-303)

In her book (Chapter 15, pg. 285) Simard refers to a student who reported that “dying Douglas firs transmitted messages to ponderosa pine … another of my students confirmed it in a second study, as did others around the world”. There are no references to published studies to support this claim, i.e., it is not corroborated by data.

Anthropomorphism: Is the attribution of human traits, emotions, or intentions to non-human entities.

Arbuscular- and Ectomycorhizal Plants: Arbuscular (AM) and ectomycorrhizal (EM) fungi form symbiotic associations with plants. Both AM and EM fungi grow inside the root. An arbuscular mycorrhizal fungus forms arbuscules (small tree-like structures) in the cortical cells of the roots but is still separated from the plant cell content by a membrane system. An EM fungus enwraps the root tips with its mycelium (mantle) and grows inside the root between the cells, encapsulating cortical cells by hyphae, termed “Hartig net”. The Hartig net is the exchange surface for nutrients. Outside the root, AM and EM fungi produce extramatrical mycelia, fine thin fungal strands or thicker root-like structures (rhizomorphs). The extramatrical mycelia can connect different plant individuals.

Common Mycorrhizal Network (CMN): A mycorrhizal network is an underground hyphal network created by mycorrhizal fungi that connects individual plants.

Consciousness: Sensory consciousness is the basic ability to have subjective experiences that can be accessed and reported. It arises from brain processes that emerged through evolutionary history (Wikipedia).

Interspecific Interference: Interspecific interference, that is when a species reduces the ability of other species to make use of a shared resource through its presence or agonistic interactions, is ubiquitous in nature. This kind of competition usually leads to restricted growth, survival and/or reproduction. However, whether tree species are less affected by interspecific competition than by intraspecific interference depends on the identity of the neighboring species and site conditions.

Mother Tree Concept: As defined by Suzanne Simard they are tall old-growth trees with vast root systems connected to hundreds of other trees via a network of fungi that allows them to share resources and information.

Myco-Heterotrotrophy: Is a symbiotic relationship between certain kinds of plants and fungi, in which the plant gets all or part of its food from parasitism upon fungi rather

than from photosynthesis. A myco-heterotroph is the parasitic plant partner in this relationship.

Plant Neurobiology: A concept based on metaphors which attempts to show that plants and animals have similar mechanisms for stimulus perception and electrical signaling. Very speculative and highly controversial.

Plate Effect: The observation that in dry seasons hardly any germinated seedlings survive around the stem of a mother tree due to its strong root competition

Self-thinning Rule: The relationship between mean tree size and tree density on a given area. It describes the decrease in stem number with increasing mean size of the trees. In a log-log diagram with diameter at breast height as a proxy for tree size it is a straight line with a slope of around -1.6.

Shamanism: Is a religion which is based on the belief that the world is controlled by good and evil spirits, and that these spirits can be directed by people with special powers (Collins Dictionary).

Wood-Wide Web (WWW): The wood-wide web refers to a common mycorrhizal network where the mycelia of mycorrhizal fungi link the roots of plants of the same or different species at the scale of a forest stand. The term originated as a cover headline in the journal *Nature* (7 August 1997), but it now appears frequently in the non-scientific literature on the subject.