Trends in Plant Science

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Opinion

Mother trees, altruistic fungi, and the perils of plant personification

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There are growing doubts about the true role of the common mycorrhizal networks (CMN or wood wide web) connecting the roots of trees in forests. We question the claims of a substantial carbon transfer from 'mother trees' to their offspring and nearby seedlings through the CMN. Recent reviews show that evidence for the 'mother tree concept' is inconclusive or absent. The origin of this concept seems to stem from a desire to humanize plant life but 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* and *Finding the Mother Tree.*

Highlights

We have analyzed the claims made in two highly popular books, which promulgate the idea that trees possess a number of human characteristics for which there is no sound scientific evidence.

A critical evaluation of the mother tree hypothesis also reveals that much of the data given in support of this concept is flawed and perhaps even non-existent. This concept is also incompatible with many well-known observations on the growth of forest trees.

Moreover, there is no evidence from peer-reviewed published studies to support the claim that mature trees in forests communicate preferentially with offspring through a common mycelial network.

It also remains unclear whether carbon compounds transmitted in the mycorrhizae actually enter the root tissue of the receiver tree. In any event, numerous studies indicate that the amounts of carbon transferred are physiologically insignificant.

> *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)

The hidden life of trees: anthropomorphism and conjecture, but not science

Probably the most well-known example of anthropomorphizing plants is the book *The Hidden Life of Trees* [1], which is a best seller with over 35 editions and is available in different languages all over the world. Wohlleben, the author of this book, 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, for which there is zero credible evidence [2,3]. 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 (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 [4]. Consequently, Wohlleben's book has been severely criticized on numerous occasions for the misinterpretation and distortion of scientific data [5–8]. We draw attention to the preface of Halbe's book [5] written

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Box 1. Caring trees and depleted soil carbon: fiction in the hidden life of trees

Since the information base of Peter 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 [77] 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 [78]. 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 [79]. 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 [80]. Ignoring such facts will lead to dense stands with low vigor trees that are highly susceptible to, for example, beetle attack, drought, fire, wind, and snow damage [81–84], as well as an understory vegetation layer with low diversity and associated lower adaptive capacity to climate change [85]. 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 [86]. 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 [87]. However, it is anything but a simple 1:1 correlation (see [88]), as Wohlleben claims in the above quote and interestingly it is the leaf biomass that 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 stabilization are unfavorable. This seems to be the case, especially on shallow sites in the Alps [89,90], or where a large part of the organic matter is stored in the humus layer [91]. 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, the soil organic matter is stabilized in the soil, a fact well-documented by soil organic matter half-lives in the range of hundreds to thousands of years [92,93]. 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 [94], but there are also studies that have found no increase in soil carbon under deadwood [95]. 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. Published results show negative (e.g., [96]), no significant [97], or even positive effects [98] of tree removal on soil carbon stocks. A current review has documented only low impacts of stand density and thinning on forest soil C stocks [86].

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 in public'. (English 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[i] and is often seen participating as a forest

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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[ii]. Wohlleben has also been appointed to the advisory board of the United Nations 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

As with Wohlleben, Suzanne Simard's book *Finding the Mother Tree* [9] has also become a bestseller. 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, a common mycorrhizal 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 carbon (C) and nitrogen (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 [9].

Does the mother tree concept 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 study conducted in Finland demonstrated that belowground competition hampers seedling establishment in boreal pine forests [10]. This has long been confirmed in many studies where mature trees have been shown to suppress growth of seedlings, for example, in maple and pine [11–13]. This finding has a long history of being acknowledged by foresters. For example, almost a century ago Aaltonen [14] 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', which has been interpreted as belowground competition from mature trees hampering seedling establishment The observation that canopy trees impede the survival and growth of seedlings has been the basis for timing of removal cuts in shelterwood regeneration systems [15,16]. In temperate beech forests, trenching, an experimental treatment preventing root competition by mature trees, has been shown to stimulate growth of the regeneration [17], a fact, established 95 years ago [18]. Fabricius [19] concluded that competition for water by overstory trees is decisive for seedling survival and growth when species-specific light requirements are fulfilled. By contrast, the mother tree concept suggests a negative impact on the offspring after trenching (i.e., in the absence of C supplied via mycorrhizal links). Thus, the mother tree hypothesis is inconsistent 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*. [20] demonstrated inter-tree net transfer of C by the use of isotopically labeled ^{13}C and ^{14}C, but the exchange mechanism remained unclear. The claim that C transfer occurred through a CMN caused a wave of enthusiasm among forest ecologists and broadened the interest in this 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., [21–25]). With the notable exception of Klein *et al*. [23] and Avital *et al*. [26], these studies conclude that only insignificant amounts of C were

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transferred to the receiver plant. Serious criticisms regarding the interpretation of the results of the study of Simard *et al*. [20] were made very early [27,28], arguing that the transfer mechanism had not been unequivocally established and that no advantage for the receiving plant had been demonstrated.

As pointed out by Robinson and Fitter [27], it is often unclear as to whether the transferred C actually enters the root tissue of the receiver tree or is simply being retained in the fungal hyphae at the root–fungal interface. In the studies by Klein *et al*. [23] and Cahanovitc *et al*. [24], label was detected in stems, suggesting C from donor trees and saplings respectively was *de facto* acquired by the adjacent trees and saplings. However, neither of these studies excluded non-CMN transfer of C. Moreover, the study by Avital *et al*. [26] used arbuscular mycorrhizal (AM) saplings to control for non-CMN transfer (a similar set-up to that of Cahanovitc *et al*. [24]) and reported significant levels of labeled C also in such saplings not sharing the same mycorrhiza [ectomycorrhizal (ECM) versus AM], pointing to the occurrence of non-CMN C transfer. Avital *et al*. [26] found C transfer of a similar magnitude between tree species that were assumed to lack mycorrhizal connections. However, some tree species have the ability for dual mycorrhizal colonization, for example, poplar can host both AM and EM species [29]. This trait may be more widespread than previously thought [30], thus permitting, in principle, linkages between AM and EM hosts. Therefore, the jury is still out on whether or not CMNs can play a significant role in C translocation under certain conditions or not.

The initial observation of bidirectional C exchange between trees under controlled experimental and field conditions [20,22] was popularized by the journal *Nature* as a cover headline to Simard's seminal article as WWW [20]. The concept of WWW linking trees in a forest by mycorrhizal hyphae received a boost when new genetic techniques suggested the presence of belowground links by the same fungal genotype among many distant trees in a stand [31]. Although the spatial 'architecture' implies physical links, intactness of the fungal connections and C distribution among trees were not demonstrated [31]. The study of Klein *et al*. [23] suggests C distribution from donor trees at stand level. As described by Henriksson *et al*. [32] the shifts in abundance of the stable isotope ^{13}C (by which transfer was assessed) that were reported by Klein *et al*. [23] were close to the magnitude of isotopic ratios that can arise from natural processes in the tree, rendering the estimates of CMN-driven C transfer uncertain. For example, release of root exudates, respiration and refixation, degradation of litter, and incorporation of the ^{13}C into amino acids [33] can result in belowground redistribution of C by soil microbes, soil fauna, and precipitation. Thus, the extent of a directed flux from a donor to a receiver is unclear.

Recent reviews have also drawn attention to the inconsistency of results obtained from experiments using different mesh sizes to include or exclude roots and mycorrhizal connections between seedlings [34,35]. In such experiments (see [20–22]), CMN 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 the authors (e.g., [21,26]) acknowledging that alternative transfer pathways could not be excluded, these studies are nevertheless often 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, from an evolutionary standpoint, 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 more closely related tree species via mycorrhizal networks (as reported by Rog *et al*. [36]) has not been generally confirmed. Indeed, facilitation may be greater when the phylogenetic distance between tree species is greater [37]. In their laboratory study, Pickles *et al*. [38] 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 C was marginal. The amount of translocated C 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*. [38] suggested that root exudates were exchanged between the compartments and likely taken up by mycorrhizae in the separated compartment.

Simard *et al*. [39] have raised the possibility that organic forms of N could represent C transferred among plants. However, even if C from a donor plant is used to synthesize organic N compounds in a CMN (mainly glutamine and arginine), any receiver plant would still spend C for the uptake of this organic N, either for direct C–N trading [40] or, at least, for energy production, which is necessary to drive the uptake of amino acids across the plasma membrane [41]. Therefore, it is unclear whether or not putative amino acid uptake from the CMN results in net C gain or loss by a receiver.

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, it is worth considering mycoheterotrophs, a group of plants that depend fully or partially on mycorrhizal fungi for their nutrition [42,43]. They acquire C (and N and other nutrients) from the fungi, which in turn receives C from a photosynthesizing host plant. As such, they represent the best example of C transfer between plants via a CMN. Mycoheterotrophy occurs both in AM and ECM plants and is the norm for orchids in early developmental stages. It is therefore possible that non-mycoheterotrophic 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 the opposite to the actual pattern of regeneration observed in forests. Moreover, an evaluation of all studies on seedling performance in forest-based CMN studies [35] found that only five out of 18 experiments 'showed significant positive CMN effects (to seedlings) that were not completely offset by negative root effects'. As discussed by Henriksson *et al*. [34], 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 AM interactions as well [44,45].

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 [40,46]. 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 question of whether such transfer would lead to a net gain or loss of C by this pathway remains unanswered.

Public reception and criticism of the mother tree concept

As with Wohlleben's book, Simard's book has also become a bestseller and has been praised by a number of plant scientists who may not have experience in mycorrhizal research. However, criticism of Simard's mother tree concept has been voiced in two major reviews [34,35]. In addition, a critical article of the work underpinning the notion of large resource fluxes between trees and seedlings through CMNs, as well as critique on the way these studies have been cited and used to build the mother tree narrative, was recently published by Jones *et al*. [47]. Their article focused on field studies of the importance of CMNs for C transfer and performance of seedlings. They noted that the two claims that CMNs are widespread in forests and that C is distributed between trees are insufficiently supported by experimental data and that alternative explanations for transfer of labeled C have not been ruled out. They also noted that targeted movement of resources and signals from large trees to genetically related seedlings, as claimed in public media, is not supported by peer-reviewed literature. Henriksson *et al*.'s [34] critique partly overlapped with that of Karst *et al*. [35] but with a stronger focus on issues with stable isotope patterns as proof of C transfer between seedlings and on the lack of molecular underpinning of the hypothesis of C transfer via CMN. They also argued that the mother tree hypothesis treats the mycorrhizal fungi as pipelines between trees, not acknowledging that they are organisms exposed to the same evolutionary pressure as other organisms. Henriksson *et al*. [34] strongly argued that in cases where isotopic patterns seem to support transfer of C between plants, alternative pathways to CMN-mediated transfer may have been in operation.

A significant part of the article by Karst *et al*. [35] is devoted to the phenomenon of citation bias in the literature, following on from the early demonstrations of a potential role of CMNs for transfer of C between plants. They identified 18 early, influential articles on C transfer in CMNs and convincingly demonstrated a trend towards bias in the citations of these articles over the last two decades; a trend towards uncorroborated statements and ignoring contradictory effects, leading to a promotion of positive effects of CMNs in forests. Further as Karst *et al*. [35] point out, 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 (Box 2). This casts great doubt on the scientific credibility of Simard's book. Despite its broad appeal, and although Simard provides a fascinating window on her life in science, her book lacks a sound scientific basis and fails to accurately 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 that 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 of the 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 of popular science books assume that fact-checking is a responsibility of the authors, but as we have seen with Wohlleben's book, self-regulation does not work. It might help if book publishers used a peer-reviewing system as in scientific journals for books categorized as non-fiction. But where commercial interests prevail, selling poorly documented narratives (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: tantalizing, but unsubstantiated hypotheses. Unfortunately, the latter promulgate a distorted and false view of the plant and fungal worlds. More dangerously, the marketing of books like those of Wohlleben and Simard by the media takes advantage of people's desire for 'harmony' and 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

Box 2. Altruistic fungi?

Many of the claims made by Susanne Simard in her book and in video presentations (TED and BBC talks *How trees talk to each other*) assume mycorrhizal fungi are altruistic, serving the needs of their plant partners. Not only is this assumption difficult to reconcile with any adaptive advantages for the fungi, some of these claims also lack supporting evidence. Several such unsupported claims presented in *Finding the Mother Tree* are detailed next.

'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) [9].

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 carbon transfer from a donor tree to a receiving tree, but it could not be verified that transfer occurred through fungal networks [23,26]. Other studies, both in the field and in the laboratory 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., [24]). Such amounts of transferred carbon are likely to be physiologically insignificant.

'Mother trees recognize their kin seedlings through the CMN.' (*Finding the Mother Tree*, pp. 259–278) [9].

A study by Pickles *et al*. [38] claims that higher rates of labeled C and N occurred in seedlings that were genetically closely related to the donor plant compared with seedlings more distantly related. But transfer occurred despite separating seedlings with a mesh that would not have allowed for fungal hyphae to connect seedlings. Also, a Master's 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[iii].

'Via the CMN, mother trees give seedlings a better chance of survival.' (*Finding the Mother Tree*, pp. 279–303) [9].

Field observations often contradict the mother tree hypothesis, which predicts a higher growth rate of seedlings in the proximity of large trees [34]. In fact, emergence and growth of seedlings and saplings are in general negatively affected by proximity to large trees [34,35].

'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) [9].

There is only one peer-reviewed study suggesting that tree seedlings can send warning signals to each other through the CMN [99]. 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) [9].

In her book (Chapter 15, p. 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). In fact, in a paper to which Simard is probably referring [99], there is no mention that the injured Douglas fir seedlings were actually dying.

The use of anthropomorphic vocabulary in science can facilitate analogies for pedagogic purposes and in literature and other media it can also be used to enhance our emotional connection with animals and plants. However, if used in a research context, it can promote a lack of scientific objectivity, with negative consequences for society. For example, in the USSR in the 1930s, Lysenko's rejection of Mendelian genetics in favor of a teleological Lamarckian view consistent with Marxism set back Russian agronomy for several decades. Scientists, as well as the general public, must avoid conflating culturally based philosophical or moral ideals with scientific reality. Anthropomorphizing fungi and plants ignore the fact that some of the most basic processes, such as reproduction, differ greatly among these kingdoms [48,49]. Nevertheless, the desire to humanize plant life has been the goal of many recently published books. Some have even adopted a shamanistic viewpoint, claiming that plants can even speak to one another and to the book's authors (e.g., [50,51]). Without experimental data to corroborate any of these claims, 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., [52,53]), but apparently can actively care for each other [9].

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 [54]), to a hearty embrace 'Yeah, I love it', (Monica Gagliano in interview with Andrea Morris [55]). However, unlike Gagliano, who suggests that this is a new way of thinking about plants, the humanization of plant function has been around for hundreds of years and has often led to controversy and confusion. Perhaps one of the best examples for this is the heated discussions in the *Academie Francaise* in the early 18th century concerning the personification of sexuality of plants (see chapter 14 in [48] and [56]). Another example is the shepherd or pastoral poetry, which in 18th century Europe conceived the ideal of a harmonious coexistence of man and nature and used an anthropomorphizing linguistic gesture for this purpose [57]. Unfortunately, the humanization of plant life continues up to the present time in the concept of plant neurobiology (see [58,59] for discussions) and has been equally controversial and fruitless.

What's at stake: anthropomorphism and its impact on forest management and ecosystem services

Even in highly-regarded newspapers, reports that promote the belief that trees are sentient beings, and thus question the idea of managing forests for wood production, are increasingly appearing [60]. 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 [61–63]. 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), an increase in imports from other parts of the world, or the substitution of wood with other materials such as concrete or steel, which typically require high amounts of fossil energy for their production [64]. 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 [65]. This necessary restoration and adaptation 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 [66].

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 [67] 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 [68], 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 [69]. If the current societal demands are not met and/or if adaptations are needed due to changed environmental conditions, then forest stands need to be adapted and restored (see, e.g., [70]). 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 [71], 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 [72]. 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 past 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 leave 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*) (see Outstanding questions).

So, why chose an anthropomorphic portrayal when this leads to lack of objectivity? In her excellent short opinion paper, Flinn [54] 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

Outstanding questions

Is there significant net C transfer via CMN that benefits recipients? This question is at the core of the mother tree hypothesis but remains to be conclusively demonstrated [27,34,35].

Similarly, it remains to be shown whether significant amounts of N can be transported via CMN from plant to plant. Pot experiments have shown that fungal distribution of soil N among the multiple plants in a CMN is related to each plant's contribution to total fungal C supply [32,45,73]. This has been shown for both AM and ECM species and the outcome is that larger plants receive more N from the CMN and that (at least among tested AM species) the presence of CMNs further exaggerate size inequality among host plants. This is counter to the hypothesized nursing of seedlings via CMN but does not address the outstanding question of how much N may move through CMN between plants.

What molecular mechanisms would enable fungi-to-plant C transfer? Here, studies of mycoheterotrophic plants may yield important clues. As these plants have not retained their photosynthetic capacity, they rely on fungi for their C uptake [74]. Mycoheterotrophs are considered parasites on fungi, but if the molecular mechanism by which they acquire fungal C were identified then analogous capabilities in other plants could be investigated.

What would be the evolutionary incentive of mediating plant–plant C transfer for the mycorrhizal fungus and what mechanisms would enable preferential plant-to-kin C transfer [40,46]? Because C transfer between plants via CMN entails that the 'donor plant' cannot exert control over the C after it has been taken up by the fungal partner [75,76], any preference for transfer to kin plants must either be indirect (e.g., higher abundance of kin plants than non-kin plants in the CMN) or else it should improve the fitness of the mycorrhizal fungi to favor kin plants.

If C transfer via CMN was conclusively shown, how can the nature of such transfer be identified? How can we distinguish partial mycoheterotrophy from collaboration?

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 [4] 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.

Declaration of interests

T. N. declares a conflicting interest as he owns shares in and works part time for the company Arevo AB that develops, produces, and markets organic fertilizers. The other authors have no conflicting interests.

Resources

[i]www.greenpeace.de/klimaschutz/klimakrise/wald-lauter-baeumen-sehen

[ii]https://ec.europa.eu/info/events/international-conference-forests-biodiversity-and-climate_en

[iii]https://open.library.ubc.ca/soa/cIRcle/collections/ubctheses/24/items/1.0103374

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