



Drought in the forest breaks plant–fungi interactions

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Abstract

Drought in the forest is not only a prolonged state of water shortage, but also an occasion where interactions between plants and fungi are affected. Water efficiency accelerates a range of pathologies in interactions between organisms, influencing the ecosystems and their interacting biological components. This study focuses on the role of mycorrhizal and endophyte fungi in alleviating the effects of soil water shortage, and on the impact of their altered activity during drought on the health of trees. The issues presented here show the fundamental role of the mycorrhizal mycelium and the mechanism of water transport to the plant in the course of other phenomena (withering, pathogenesis, endophytes biology) that occur in trees under influence of drought, with particular attention on managed coniferous stands. Conclusions resulting from published information on this topic emphasize the negative impact of soil moisture deficiency on the ectomycorrhizal fungi functioning and, in contrast, on the promotion of the growth of some endophytes, pathogens and hemi-parasitic mistletoes (*Viscum* spp.).

Keywords Water deficit · Nutrients · Mycorrhiza · Endophytes · Transpiration · Tree vitality · Pathogens · Forest dieback

Introduction

Maintaining forests in good health under conditions of global climate change is one of the most critical challenges faced by foresters. Although rainfall intensity and frequency increased in the Northern Hemisphere in the second half

of the twentieth century, many areas were also affected by drought (Stocker et al. 2013). Drought is increasingly observed in connection with the global water crisis resulting from climate change, while it is also attributable to human activities, e.g., because of influence on ground water, deforestation, and inappropriate land drainage (Lenton and Muller 2012). The massive devastating wildfires in many regions of the world are the most alarming example of drought caused by climate change. This dangerous phenomenon is also observed in Central and Northern Europe (Škvarenina and Vida 2009; CTIF 2019; Krikken et al. 2019; Venäläinen et al. 2020). In Poland as example, the area of forests seriously affected by drought has been increasing and, in 2018, was estimated to have affected 43.5 thousand hectares of forest (Zajączkowski et al. 2019).

Coniferous forests occupying the Central European lowlands, however, adapted to local growing conditions, they are nevertheless vulnerable to harmful effects of climate change (Vitali et al. 2018). Most of these forests, especially stands with domination of *Pinus sylvestris*, grow on poor sandy soils with low water retention capacity, which increases the risk of drought as the climate is becoming warmer. These stands receiving relatively low rainfall, react the fastest to the lack of water in the soil, to low precipitation, and long-lasting insolation.

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The increased risk of drought on forests, which is associated with global climate change, is indicated by the average annual rainfall of < 600 mm and noted in 313–316 sub-provinces of Germany and Poland (Banaszkiewicz et al. 2008; Panka 2012; Solon et al. 2018) and in other countries in Europe, as well (Caloiero et al. 2018). Forests in the European regions influenced by both maritime and continental climates, are more susceptible to altered weather conditions. Planting tree species that have greater resistance to high temperatures and drought may, however, result in severe frost damage, since below freezing temperatures may occur in the European lowlands even in late May (Körner et al. 2016; Agafonova et al. 2017). Given that trees have life spans of more than 100 years, the risk of high losses due to reduced soil moisture and adverse weather conditions over the coming century is substantial (Lindner et al. 2010). In addition, some tree species, especially conifers, were used in large-scale afforestation—in Poland and East Germany on post-agricultural soils or in Ukraine in the steppe zone. In such habitats the trees still are not fully productive or resistant (Soloviy 2000; Wegehenkel 2003; Sierota 2013).

To present the overall complexity of the impact of drought on tree mortality, it is necessary to clearly explain the course of this process, which occurs simultaneously in the roots, trunk, and the crown of the tree (Davi and Cailletet 2017). Considering the genetically and epigenetically encoded regulation of trees' resistance, to better understand forest drought, we should pay special attention to the soil microcosm which is connected to the uptake of water by the roots and, indirectly also its transpiration in the crowns of trees (Hagedorn et al. 2016). The xylem water conduction has well known physical nature but is strongly influenced by the surface and activity of mycorrhizal mycelium in the soil and the presence of some fungi in the vessels and coils of inhabited wood (Abdullah et al. 2017), which

in turn may contribute to disrupting the water flow up the tree. Figure 1 abstracts the fungal role in this process in the drought condition.

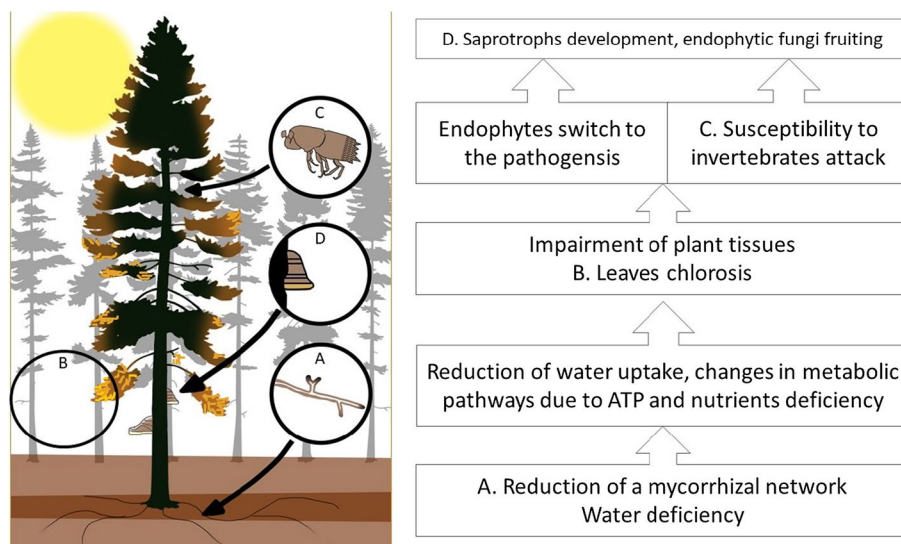
The present work reviews the state of knowledge on changes occurring in the trees during drought in coniferous stands in central Europe. Emphasis is paid to the different role of mycorrhizal fungi, as well as endophytes and pathogens in trees under stress condition. These dependencies are not sufficiently known to both forestry practitioners and forest managers. Research is rare that simultaneously observes the tree crown and the root system.

To review the analysis of drought impact on forests in Central Europe and its relations to fungi, the databases in Scopus, Google Scholar and Web of Science were browsed. Broad literature focusing on response of specific fungi to the drought and climate change was found—more than 607 thousand articles for mycorrhiza, however records of works focusing on drought-stressed plants in the context of co-occurring fungi (mycorrhizal, endophytic, and pathogenic ones) were much rarer. The objectives were focused on general information about the role of mycorrhiza and fungi inhabiting drought-stressed trees with special references to water uptake. We also tried to identify gaps in research and possible future methods of trees' protection against drought.

Drought in Central Europe in the last decade and climate change forecast

The average global air temperature in 1880–2012 increased by 0.85 °C, and the first decade of the twenty-first century is the warmest since instrumental measurements began (IPCC 2013). One of the effects of global warming is the increased intensity, duration, and area of drought since 1970. On a global scale an increase in the percentage of annual drought

Fig. 1 Diagram showing the order of changes in the health condition of trees in drought conditions (drawing: M. Wrzosek)



periods experiencing many different areas from 1902–2008 has been observed (Wang et al. 2014). Particularly acute was a drought in Europe in summer 2003, when heat was extremely high (Burke et al. 2006; Rebetz et al. 2006; Blunden et al. 2011). In central Europe, it is anticipated that climate change will result in warmer temperature and lower rainfall during the growing season (Briffa et al. 2009; Dubrovský et al. 2009). The Soil Moisture Anomaly (SMA), an indicator of agricultural drought conditions compiled by the JRC European Drought Observatory (EDO), shows that droughts beginning in spring of 2015 and 2018 affected Germany, Greece, western Poland, and Scandinavia (Masante and Vogt 2018; Masante et al. 2018; Spinoni et al. 2018). In September 2018, drought had been relieved in Scandinavia, but had appeared west to cover France, remaining also in Poland (Masante et al. 2019). Drought Severity Index (DSI) for 10-day periods from April to July 2015 shows a gradual increase from mid-May in many parts of Europe. In May 2015, the drought covered Germany and western Poland, after which drought spread in all directions and increased its severity, covering almost all of Europe, except Scandinavia. In 2018, Central Europe experienced one of the most severe and long-lasting summer drought and heat wave ever recorded. Before 2018, the 2003 millennial drought was often invoked as the example of a “hotter drought” and was classified as the most severe event in Europe for the last 500 years (Schuldt et al. 2020). First insights now confirm that the 2018 drought event was climatically more extreme and had a greater impact on forest ecosystems of Austria, Germany, and Switzerland than the 2003 drought (Schuldt et al. 2020). According to monitoring by JRC EDO, drought occurred in Europe again in 2019. They determined that several regions spanning from northeast to western Europe experienced drought conditions, including Lithuania, central Poland, Czech Republic, Germany, central France, and central Spain (Masante et al. 2019). Droughts in Poland were described in detail by Zajączkowski et al. (2019), based on a modified climate water balance indicator and the number

of days with limited soil water availability. In the periods assessed, the best moisture conditions for the growth of forest stands occurred in Poland in 2010, 2013, 2017, while the longest droughts, covering large parts of the country, occurred in 2015 and 2018 (Fig. 2). In 2015 a large moisture deficit covered almost the entire country (Boczoń et al. 2016). The climatic water balance of the warm half-year showed a moisture deficit exceeding 200 mm. A moisture shortage in the summer months in 2015 covered 87% of Poland. Based on the annual climate water balance of forested areas, moisture deficits (mean 140 mm, up to 300 mm) occurred in 2018 in both western and southeastern Poland. A more detailed analysis shows the increasing risk of drought also in the east, as well as in the central part of the Baltic coastal areas (Boczoń, unpublished).

According to the InterSucho project, which maps the occurrence of drought in the Czech Republic, in July 2019, 63% of the country was seriously affected (Fraňková 2019; InterSucho 2019). Climatic anomalies causing drought are a great threat to forest ecosystems: in the warm half of the year, soil water decreased because evapotranspirational losses generally exceed precipitation and leads to faster soil water depletion. European Environment Agency publishes the current drought prognosis for the continent up to 2100 and states that the frequency and severity of droughts will be increased in most parts of Europe. The maps illustrating the problem are shown on the webpage: <https://www.eea.europa.eu/data-and-maps/indicators/river-flow-drought-3/assessment>.

Responses of host-plants and mycorrhizal fungi under drought conditions

Mycorrhiza is a mutualistic symbiosis between a plant's roots and a specific fungus, which plays an integral role in the root–soil interface, influencing nutrient cycling and shaping terrestrial ecosystems. Mycorrhizal fungi are widely

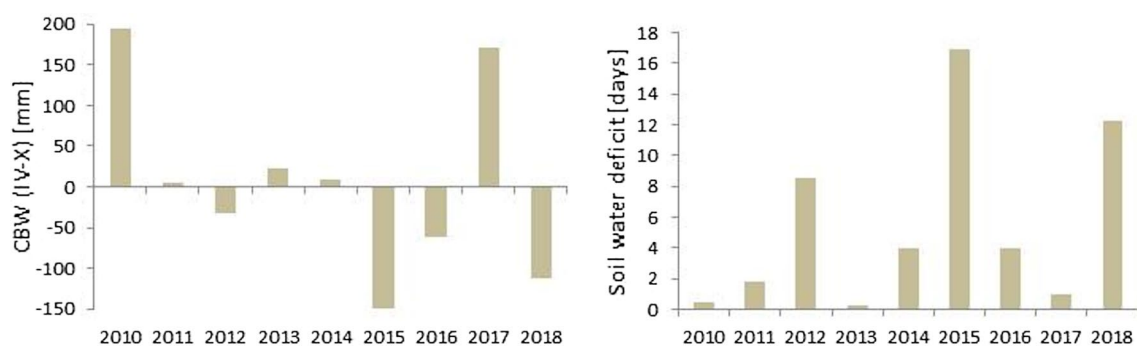


Fig. 2 Average drought indices weighted by the area affected in Poland, left—climatic water balance (CWB) for April–September, right—number of days with soil water deficit from May to July (A. Boczoń, unpublished data)

distributed in different types of terrestrial ecosystems and include several groups, forming, respectively, to own properties different types of fungus–plant interactions, known as ectomycorrhiza (EM), arbuscular mycorrhiza (AM), ericoid, orchid mycorrhiza, and others. Fungal–plant symbiosis is often context-dependent and differentially responds to the water depletion's stress. Mycorrhizal associations are formed by plants and fungi from different taxonomic groups, but only ectomycorrhiza (EM) occurring between woody plants and asco- and basidiomycetous fungi produces pronounced mantle, Hartig net and large extrametrical mycelium (Schubert et al. 1987; Song et al. 2007; Smith and Read 2008). The initial stage of mycorrhiza formation includes a signal exchange between the two symbionts, physical connection, and functional integration (Kowalczyk and Hryniewicz 2018). In EM symbiosis (Blasius et al. 1986; Taylor and Alexander 2005), this integration consists of: (1) the Hartig net, responsible for the direct transfer of water and minerals into plant cells, in exchange the fungus receives carbohydrates and other compounds necessary for mycelium growth, (2) a hyphal mantle around the root, providing structural protection, increasing the absorbing surface and storing moisture, (3) a hyphal network of extrametrical mycelium, penetrating the soil at a speed of up to 4 mm/day (Fig. 3). This type of mycorrhiza is usually strongly affected by drought but at the same time its state could be crucial for tree resistance to drought. In AM symbiosis, fungi form a specific appressorium called hyphopodium which penetrates the root through the pre-penetration apparatus, which guides the fungal hyphae through the root cells toward the bark (Parniske 2008; Krishnakumar et al. 2013). In the cortex, the hyphae enter the apoplast and grow laterally along the root axis,

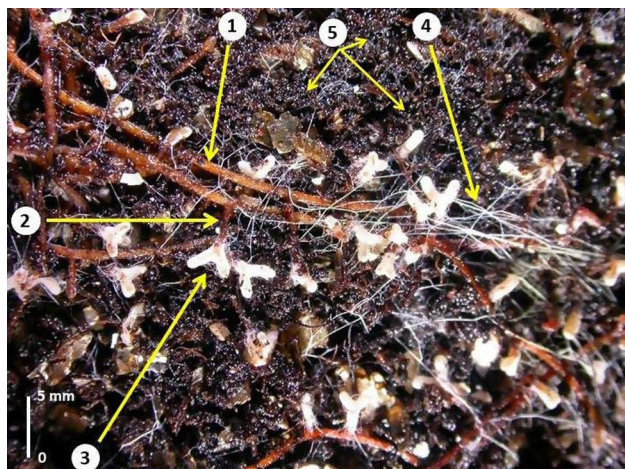


Fig. 3 Scots pine roots with *Scleroderma citrinum* mycorrhizae in soil. 1–n-order roots, 2–lateral n+1 roots, 3–dichotomous mycorrhizal roots with mantle, 4–ectomycorrhizal extrametrical mycelium, 5–individual hyphae, visible as white spots that are reflections of light (Photo: D. Hilszczańska)

occupying inner root cortical cells. The intracellular hyphae form structures by repeated branching known as arbuscules that are considered as the site of nutrient exchange. While arbuscular mycorrhizas are the most common form of mycorrhizal interactions occurring in the roots of approx. 65–90% of all land plant species including flowering plants, bryophytes, and ferns (Zhu et al. 2010), the mechanisms controlling arbuscule development are still largely unknown (Paszowski 2006). The AM mycorrhiza is less influenced by drought. A normally developed root system of temperate tree species usually forms symbiotic associations with EM fungi (Bonfante and Genre 2010; Cosme et al. 2018), but arbuscular mycorrhizae are also important because they can interact with them. The two types of mycorrhizae (AM and EM) can coexist with one plant species including *Populus* spp and *Pinus* spp improving the state of plants under drought conditions (Teste et al. 2020, Karlst et al. 2021).

Mycorrhizae and water uptake

Mycorrhizal symbiosis plays a major role in two plant processes: water–mineral absorption and the allocation of carbon within the plant, with some carbon compounds ultimately transferred to ectomycorrhizal fungi (Guehl and Garbaye 1990; Simard 2003; Courty et al. 2010). Ectomycorrhizal plants often have higher nutrient contents than non-mycorrhizal plants, especially when grown in soils with low nutrient availability. This is the typical condition of pine stands located on poor sandy soils in many European countries, where the ectomycorrhizal net also substantially improves the uptake of water by trees (Jones et al. 1990). Roots with associated extrametrical mycelium can explore a larger volume of soil than non-mycorrhizal roots, and hyphae can explore small soil pores that are not accessible to plant roots (Garbaye 2000; Lheto and Zwiazek 2011), thus improving plant water status under low soil moisture conditions (Morte et al. 2001; Duñabeitia et al. 2004). However, some authors have failed to find a beneficial effect of ectomycorrhizal fungi in dry conditions, suggesting that both plant and fungus can be directly limited by water availability (Dosskey et al. 1991; Kennedy and Peay 2007; Peay et al. 2015). Drought may reduce fungal growth and limit its ability to supply the plant with nutrients. Simultaneously, the plant responds to drought by limiting carbon flow to the roots, suppressing the fungal symbiont. It has been experimentally shown that plant response to drought varies considerably depending on the associated fungal species (Lamhamedi et al. 1992). Recent data suggest that fungal transmembrane water channels, i.e., aquaporins, regulate the acquisition and release of water by the hyphae, and therefore could induce drought tolerance (Xu and Zwiazek 2020). Ectomycorrhizal fungi have different capabilities for transporting water. Barnes et al. (2018) suggest that some

fungi do not respond favorably to saturated soil moisture conditions, regardless of their role in its transport. The ability to colonize a host root is also greatly affected by water supply. In microcosms of Scots pine (*Pinus sylvestris*), the colonization abilities of three ectomycorrhizal species, viz., *Thelephora terrestris*, *Laccaria laccata* and *Hebeloma crustuliniforme*, were insensitive to flooding, whereas *Suillus flavidus* and *S. bovinus* were sensitive (Stenström 1991). Plamboeck et al. (2007) found species-specific effects of ectomycorrhizal fungi on hyphal transport of water. In the test performed with isotope and fluorescent dye analysis, only one of 15 ectomycorrhizal fungal morphotypes was able to transfer stained water to Douglas-fir seedlings. In work by Prieto et al. (2016), *T. terrestris* hyphae enhanced interplant transfer and redistribution of water between *Pinus halepensis* saplings and seedlings whereas *Suillus granulatus* did not.

Arbuscular mycorrhizal fungi (AM) are able to strengthen the growth of host plants especially under stressful conditions by mediating a series of complex communication processes between the plant and the fungus leading to increased photosynthetic rate and other gas exchange-related traits (Birhane et al. 2012). Plant tolerance to drought could be primarily due to a large volume of soil explored by roots and the extra-radical hyphae of the fungi (Gutjahr and Paszkowski 2013). There is an extensive literature on plant responses to AM inoculation on host species exposed to drought. For example, *Glycine max* L. growing in water stress conditions after inoculation with AM enhanced leaf proline, photosynthesis, leaf area index, relative growth rate, fresh weight, and dry weight of seeds (Pavithra and Yapa 2018). Ouledali et al. (2018) showed that AM alleviated drought impact and increased turgor potential (Ψ_p) and mineral uptake of olive trees (*Olea europaea* L.). Increased dry biomass, water usage effectiveness and net photosynthetic rate of *Robinia pseudoacacia* L. seedlings inoculated with AM fungi (*Funneliformis mosseae* and *Rhizophagus intraradices*) have been observed (Yang et al. 2014). Numerous evidences of improved resistance also to salinity, herbivory, temperature, heavy metals pollution, and diseases due to fungal symbiosis have been reported (Rodriguez et al. 2008; Salam et al. 2017).

It is worthy to notice the results obtained by Morgado et al. (2015, 2016). The authors show the possible shift in composition of mycorrhizal fungi in Arctic ecosystems with different depths of snow cover and different temperatures. A relevant adaptation of ectomycorrhizal fungi is the degree of hydrophobicity of their below-ground structures, and the plasticity of this property in response to environmental conditions. Some species of fungi produce hydrophobic rhizomorphs that facilitate transport of soluble substrates and water (Unestam and Sun 1995), and hydrophobicity is likely to be a trait that provides stress tolerance for soil-borne

fungi. These remarks should be a guideline in searching for more resistant mycorrhizal fungi.

Depending on fungal species, ectomycorrhizal fungi differ in the anatomy and morphology of the mycelia radiating into the soil, and these morphological variations are believed to be related to ecological functions and modes of foraging exploration (Agerer 2001; Shahin et al. 2013). It has been suggested that ectomycorrhizal root tips with hydrophobic mantles and highly differentiated extensive external mycelium (i.e., so-called rhizomorphs, developed by *Boletus* and *Cortinarius* genera), are resistant to drought and effective at water transport and uptake for their hosts (de Jalon et al. 2020). Some species of the genus *Cortinarius* are specially adapted to dry conditions, probably due to the characteristics of their mycelium, which are hydrophobic and much more persistent than mycelium of other mycorrhizal fungi, for example those belonging to the genus *Tomentella*. Moreover, *Cortinarius* spp. excrete Mn-dependent peroxidases, which participate in enzymatic oxidation of humus to release nutrients from dead organic matter in northern forest ecosystems. The abundance of *Cortinarius* spp. is likely to increase with climate change, including in northern hemisphere forests (Bödeker et al. 2014).

Gehring et al. (2017) found that ectomycorrhizal community composition is under strong plant genetic control. Inoculation experiments have shown that ectomycorrhizal communities are critical to plant drought tolerance. Both drought-tolerant and drought-intolerant seedlings grew similarly when provided sterile ectomycorrhizal inoculum. However, drought-tolerant seedlings grew 25% larger than the drought-intolerant seedlings under dry conditions. Each seedling type developed its distinct ectomycorrhizal community. This outcome demonstrates that combinations of plant genotype and ectomycorrhizal communities improve the survival and growth of trees under drought, which is of great importance due to the vulnerability of forests around the world to the warmer and drier climates predicted for the future (Pilosof et al. 2017). Since the fungal EM network connecting plants stabilizes the ecosystem, as shown by Simard (2009), the composition of drought-tolerant trees and drought-tolerant fungi, especially those that can connect with different partners, may be a crucial issue in future forest design.

Mycorrhizae and nutrients uptake

Functional variation exists among taxa of ectomycorrhizal fungi in the ability to utilize different nutrient sources to obtain nitrogen (Abuzinadah and Read 1989; Jones et al. 2009) and phosphorus (Colpaert et al. 1999). Fungal species can be characterized in terms of their capabilities for nutrient acquisition under given environmental conditions, based on the specific extracellular enzymes involved in degradation of

celluloses, hemicelluloses, chitin and proteins, the oxidation of phenols and the mobilization of phosphorus (Courty et al. 2005; Pritsch and Garbaye 2011).

According to Harley (1989), mycelium use 30% of the carbon assimilated in the process of photosynthesis by the plant. Van der Heijden et al. (2015) stated that up to 80% of nitrogen and up to 90% of phosphorus requirements of plants are acquired by mycelium. The presence of ectomycorrhizal mycelium (including emanating elements) is strongly correlated with higher phosphorus levels in young trees (Rousseau et al. 1992). Feedback between mycorrhiza and a tree affects the state of the crown and the condition of its roots, including mycorrhizal tips and extramatrical mycelium (Fig. 4). Phosphorus is assimilated by both types of mycorrhizae by solubilization of inorganic phosphorus and hydrolysis of organic phosphorus from soil (George et al. 1995; Hilszczańska et al. 2008; Hilszczańska 2009). Its uptake by trees is improved effectively by AM fungi. It should be an appropriate practice to plant some species that exhibit two types of mycorrhizae (EM + AM) or to encourage the growth of herbaceous plants in forests that can associate with EM mycelium. Fern *Pteridium aquilinum* is often seen as a kind of weed in forests (Milligan et al. 2016), with strong competitive properties but also is a plant that connects with trees through the mycorrhizal network (Conway and Arbutnott 1949; Acsai and Largent 1983; Ouden 2000). The negative impact of *Pteridium* on herbaceous plants can be balanced by the improvement of trees' roots state. The effectiveness of mycorrhiza in promoting the growth and nutrition of trees depends on an association with a suitable ectomycorrhizal fungal species, even down to strain. Along with the abundance of ectomycorrhizae, the amount and degree of differentiation of extramatrical mycelium is an important ecological factor underpinning tree performance (Colpaert

et al. 1992; Thomson et al. 1994). The negative effect of drought on potassium uptake was shown in several studies (Agerer 2001; Smith and Read 2008; Van der Linde et al. 2018). It was found that ectomycorrhizal fungi with hydrophobic mycelium transfer more potassium ions than those that have hydrophilic mycelium. Danielsen and Polle (2014) revealed that young poplar (*Populus × canescens*) growing under dry conditions had higher levels of phosphorus and other cations, in particular potassium, in shoots of ectomycorrhizal plants, but not in roots. Similarly, Mg increased in roots regardless of ectomycorrhizal status, whereas foliar concentrations of Mg increased only in ectomycorrhizal plants (Danielsen and Polle 2014). The activity of both EM and AM fungi aids in preventing salt-induced ion toxicity while alleviating nutrient deficiency (Kapoor et al. 2013).

It is also known that higher CO₂ levels in laboratory conditions change the composition and influence of the microbial community in soil. AM fungi, e.g., of the Gigasporaceae family, have positive effects on plants under conditions of elevated CO₂, whereas elevated CO₂ has strong negative effects on Glomaceae fungi. A CO₂-enriched atmosphere, which causes the greenhouse effect, can reduce the benefits of mycorrhizae, negatively affecting plant functionality (Johnson et al. 2005).

The functioning of mycorrhizal systems and their role as donors of mineral compounds to trees is often discussed in the context of the impact of nitrogen on tree growth, with regard to eutrophication of habitats, in stands varied in tree density, or on the increase in stand growth and tree abundance (Socha and Orzeł 2013; Saarsalmi et al. 2014; Staniaszek and Socha 2015).

Climate change will strongly affect nitrogen flow. Drought increases soil aeration and thus makes conditions unfavorable for N₂O production by denitrification (Castaldi 2000).

Fig. 4 Diagram illustrating ectomycorrhiza of *Aureobolus projectellus* (a) with extramatrical mycelium (b) and *Pinus sylvestris* fine root (c). Extramatrical mycelium penetrates the capillary spaces of parent soil particles (1), mineral (2) and organic (3) compounds filled with water solution (M. Wrzosek)



The projected changes in precipitation and temperature will affect emissions of N_2O and NO from the soil. Also, drought limits the overall activity of soil microorganisms, reducing the amount of N cycled in the ecosystem (Kieft et al. 1987) and promotes nitrogen accumulation in forest soils by reduction of the litter decomposition rate (Wieder et al. 2009). Also, Sanaullah et al. (2012) found that drought reduced the release of C and N from litter by more than 50%. For EM mycelium, soil nitrogen is absorbed in the form of both organic and mineral nitrogen; nitrogen is transferred to roots and other tree tissues, promoting plant development, and participating in biomass production. Nitrogen is particularly easily absorbed as ammonium, which is released from the soil substrate with the fungal enzyme glutamine synthetase and transferred to root cells in the form of the amino acid glutamine, which is necessary in many nitrogen cycles and in protein biosynthesis (Marschner and Dell 1994). Excess nitrogen in the soil solution increases its absorption by hyphae, but at the same time causes the consumption of carbon from carbohydrates supplied by the host plant and affects EM equilibrium (Hobbie and Colpaert 2003). Global warming scenarios also project an increase of nitrogen in forest ecosystems due to its airborne deposition and use of fertilizers. The presence of fungi can improve the equilibrium removing nitrogen (predominantly in organic form) from the soil. Some field studies show the phenomenon of the decrease of inorganic nitrogen level in soil with elevated temperatures (Lilleskov et al. 2002; Avis et al. 2008; Pickles et al. 2012). The presence of fungi which can link plants with organic sources of nitrogen can be especially desired.

Water transport under drought

Mycelium of the ectomycorrhizal fungus penetrates the capillary spaces (pores) between the mineral-organic structures that form the soil, acquiring water and soluble mineral compounds by osmosis. The transport of water from the soil to the leaves occurs through an unbroken column of water from the soil into the cells of the fungus, from there into root cells, then into water conducting xylem tissues up to the leaves. Transpiration taking place during the day in the leaf creates a water potential gradient that induces the influx of water from the soil into the fungus hyphae network and up the tree to the transpiring leaves (Egerton-Warburton et al. 2007a, b). The hyphal networks produced by ectomycorrhizal fungi are apparently adapted for water transport (Johnson 2018). The total length of mycorrhizal mycelium on a tree root system can reach hundreds of meters in length, with up to 4000 m of hypha per linear meter of roots (Read and Boyd 1986). For example, hyphae of *Suillus bovinus* can reach a total of 200 m in 1 g of soil, with the length of single hyphae of *Thelephora terrestris* reaching up to 20 cm, and *Pisolithus tinctorius* hyphae can extend up to 42 cm from a mycorrhizal

root (Hilszczańska and Sierota 2005; Nedelin 2014). Early studies using isotopically labeled water provided evidence that rhizomorphs of *S. bovinus* facilitated apoplastic transport of water through their central vessels. This transport was directed to several plants connected to the hyphal network and was especially efficient for coniferous seedlings (Duddridge et al. 1980). Based on pioneering early work by Duddridge et al. (1980) and Brownlee et al. (1983), sets of experiments have been developed to demonstrate how common mycorrhizal networks (CMNs) can facilitate interplant transfer of water between seedlings both in the field (Warren et al. 2008) and in laboratory (Egerton-Warburton et al. 2007a, b).

Mycorrhizal fungi often form a symbiosis with different tree species, so the extrametrical mycelium creates a type of mycorrhizal system, where young seedlings benefit from being connected with older trees (Dighton and Mason 1985; Agerer et al. 2012). In a state of soil water deficiency, young mycorrhizal plants can fix CO_2 at a rate ten times greater than that of non-mycorrhizal seedlings, as shown by Parke et al. (1983).

Water is a good solvent due to its polar properties and differences in solute concentrations across semipermeable cell membranes create a cellular osmotic potential gradient that can cause water and ion movement. Ions can also move against an osmotic gradient through protein ion channels or protein conveyors. Leaf transpiration, driven by differences in water potential of air and stomata of leaves, is the driving force of passive transport by diffusion. According to Lheto and Zwiazek (2011), water transport occurs via the symplast in at least five pathways, via plasmodesmata connecting protoplasts in adjacent cells, and via the apoplast along cell walls. During dry periods, when osmotic concentrations of the soil solution may exceed those in the mycelium, active transport occurs in which the ion concentration gradient is overcome by ATP regulation. An essential energy carrier of the then-activated proton and/or ion pumps is ATPase, in the mycelium and root cells. Active transport regulates the amount of nitrogen and phosphorus in the cellular structures of the fungus and root cells (Lum and Hirsch 2002; Krajinski et al. 2014). Drought is, in consequence, a period of intensive energy consumption and only plants and fungi storing the supply can survive harsh time. The fungi store energy in the form of oil and glycogen. If a part of the mycorrhizal net is richer in these compounds than others, it can be available to other fungi and plants, as long as the mineral and energy compounds are translocated by hyphae. The high stoichiometric status of N:P is also recognized as a factor influencing transport of mineral compounds from plant to plant via mycelium (Mariotte et al. 2017).

Mycorrhizal systems, however, are subject to damage for many reasons, not only related to natural death, but also due to external disturbances, such as pathogens,

consumers, mechanical damage, or toxins. An important element in these processes is the disruption or cessation of the water and ion uptake due to drought. The presence of root pathogens is an important factor reducing root water uptake. These pathogens do not directly colonize fine roots, but by infecting woody, thicker parts, they cause the death of living tissues, including phloem. Infection of thicker roots and cell degradation caused by the pathogen's enzymes cuts off access to carbohydrates for the mycorrhizal mycelium, which in turn reduces water transport to this part of the root system (Graham 2001; Piri 2003). There are some remarkable reports (e.g., Simard 2016; Defrenne and Simard 2019) of trees in conditions of moisture deficiency surviving harsh time due to the link to the mycorrhizal net. Water not only is a carrier of ions and other metabolic compounds in trees, but more importantly is an electron donor in photosynthesis (Kopcewicz and Lewak 2019). Transpiration regulates the thickness of cuticles and stomata in the lower surface of leaves or needles. Water vapor transpiring through stomatal apertures cools the surface of the leaves on the one hand and regulates the water status of the plant on the other. Wind, insolation, and humidity, as well as soil water content, significantly affect transpiration (e.g., Taiz and Zeiger 2006). Stomatal closure in the event of drought regulates water loss by perennial woody plants. The opening of stomata occurs when there is increased turgor in the guard cells due to the influx of water. This influx is, in turn, the result of ionic changes in the stomata due to glucose loss, caused by its breakdown or natural use (Daszkowska-Golec and Szarejko 2013). Drying of the tree crown influences the state of the roots and mycorrhizal partners, and vice versa (De Boer and Volkov 2003; Kopcewicz and Lewak 2019). In conditions of increasing soil drought and changes in the ionic concentration of the soil solution, progressive changes in the activity of mycorrhizal mycelium also determine physiological and pathogenic changes within the crown. This activates co-existing endophytic fungi and pathogens first of all.

Endophytes and drought

Endophytes inhabit practically all parts of plants, from roots to shoots and leaves. Endophytic fungi have been classified into two broad groups (clavicipitaceous and non-clavicipitaceous) based on their phylogeny and life history traits (Rodriguez et al. 2009). The clavicipitaceous endophytes are all phylogenetically related and proliferate within cool and warm season grasses (Saikkonen et al. 2016). The non-clavicipitaceous endophytes which are from woody plants belong to the Ascomycota or Basidiomycota group (e.g., Sieber 2007; Watkinson 2016). They are significant for plants due to their common occurrence in forest stands and performing important physiological and ecological functions

(Arnold 2007; Unterseher 2011; Witzell and Martín 2018; Hodkinson et al. 2019). Endophytic fungi colonizing leaves or shoots cause various biochemical effects on their host—when water is scarce, endophytic fungal enzymes consume nutrients from the cells of the tree, which reduces the activity of plant cells and can cause, for example, chloroplast degradation and chlorophyll destruction, magnesium deficiency and nitrogen excess (Schulz et al. 2002; Mousa and Raizada 2013). Endophytes, on the other hand, are conversely activated under unfavorable conditions in the production of gibberellins or many other compounds (Arnold 2007, 2008; Kusari et al. 2012; Khan et al. 2015). Root endophytic fungi, unlike mycorrhizal fungi, colonize all parts of the internal root system, which means that their biomass is even higher than that of mycorrhizal fungi (Grünig et al. 2006, 2011; Bartnik 2013). However, because they can improve the nutrient status and water balance of the host plant (Likar 2018), their role in plant development is no less important than that of mycorrhizal fungi (Hilszczańska 2016; Stroheker et al. 2018; Khullar and Reddy 2019; Rana et al. 2019; Landolt et al. 2020).

Interactions between host and endophyte species are forms of mutualistic symbiosis or commensalism, but visible symptoms arise when plants are under stress (Watkinson 2016). Endophytic organisms usually benefit their hosts by increasing plant stress tolerance (Rodriguez and Redman 2008), or by reducing the possibility of insect attack by producing toxic alkaloids (Zhang et al. 2012; Lugtenberg et al. 2016), or by reducing infection of plant tissues by pathogens due to antagonism (Arnold et al. 2003). However, some endophytic fungi, depending on the fungal development stage, plant growth phase, weather and environmental factors and host reaction, can become pathogens (Schulz and Boyle 2005; Sieber 2007). In recent years, one of the most important abiotic factors damaging European forests directly and indirectly (activation of needle and stem endophytes) has been water shortage. It was associated with long periods of drought and accompanying high air temperatures (Allen et al. 2010; Sierota et al. 2019) what changed the balance between plant and an endophytic fungus. An example of a fungus with an endophytic stage found in the shoots and needles of *Pinus* spp., which is activated by water stress, is *Cenangium ferruginosum* (Fig. 5a). Its presence can cause pine dieback when conditions become favorable to the fungus or unfavorable to the host (Jurc et al. 2000), although Ryu et al. (2018) did not show a direct effect of drought on the induction of *C. ferruginosum* pathogenicity. However, they found that under water deficit, the resistance to infection of pine decreases as well as the presence of some terpenoids, flavonoids, and phenolic acids (Jurc et al. 2000; Kunca and Leontovyč 2013b). At the same time, accumulation of abscisic and jasmonic acids in plant is observed (Ryu et al. 2018). This condition of the tree facilitates the

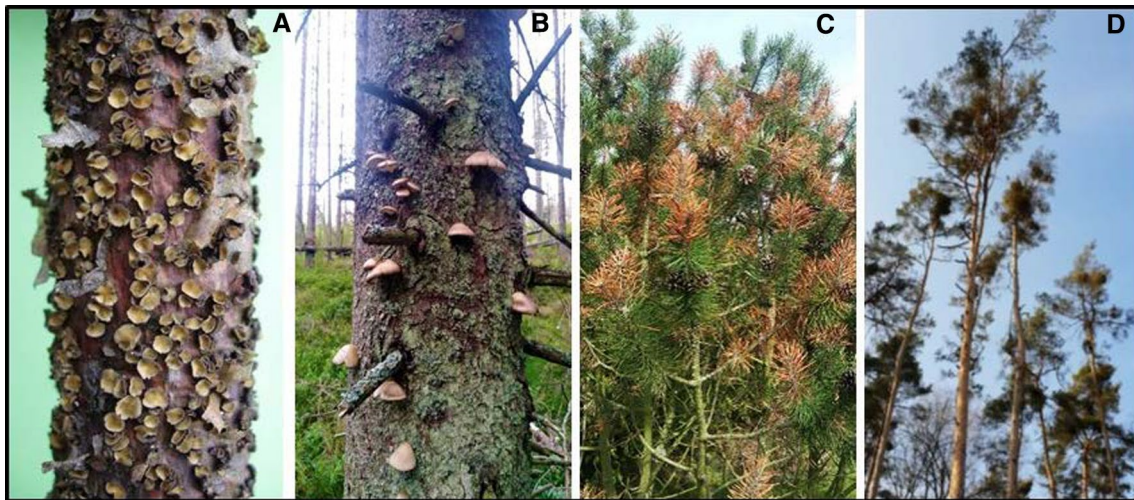


Fig. 5 a—Numerous apothecia of *Cenangium ferruginosum* on a branch of a dead *Pinus sylvestris* previously weakened by drought (Photo: A. Szczepkowski); b—*Pleurotus abieticola* basidiomata occurring on standing spruce after drought and infestation by spruce bark beetles, Tatrzanski National Park, 2019 (Photo: M. Wrzosek);

c—crown of *Pinus mugo* growing in water deficiency and infected by *Sphaeropsis sapinea* (Photo: A. Szczepkowski), d—droughted Scots pines with numerous mistletoe in the crown (Photo: courtesy by K. Nowik). Photos at different magnifications

growth and development of *C. ferruginosum* and causes a change in its biology. The fungus shifts from endophytic phase to phytopathogenic and saprotrophic lifestyle (Kunca and Leontovyč 2013a, b). *Sphaeropsis sapinea* (syn. *Diplodia sapinea*) causing *Diplodia* tip blight (shoot dieback of conifers) (Fig. 5c) is also a relevant example of fungus which can change its lifestyle from endophytic to pathogenic when climatic conditions change with precipitation deficits and increased temperatures. The mentioned climatic conditions that weaken trees, together with the properties of *S. sapinea*, probably are largely responsible for its rapid spread and increasing coniferous forest health problems in Northern and Central Europe (Fabre et al. 2011; Brodde et al. 2019; CABI 2019; Sierota et al. 2019; Bußkamp et al. 2020; Szczepkowski et al. 2021).

In Poland in the end of the twentieth century, the large-scale death of Scots pines (ca. 1 million ha) was a consequence of frost drought at the end of winter. Rapid transition from low to warm temperatures, which evoked high rates of transpiration in the needles and simultaneously a lack of water provided by root systems because of still frozen soil was catastrophic for trees (Kowalski 1997; Sierota 2011; Sierota et al. 2019). At the same time, there were large-scale outbreaks of the endophytes *Thyronectria cucurbitula* and *C. ferruginosum*, and the damaging insect *Contarinia baeri* (Sierota et al. 1998).

Adverse environmental conditions usually do not occur singly, but often arrive with other unfavorable conditions or they arrive one after another. One consequence of dry and hot conditions is an increased occurrence of forest fires. In Poland in just one year of 2019 over 9,600 forest fires were

recorded (Zajaczkowski et al. 2020). Pine trees, weakened not only by water stress but also damaged by fire, may be subsequently attacked by numerous occasional weak parasites and pathogens, including endophytic fungi, such as *C. ferruginosum*, *Pezicula cinnamomea*, *Thyronectria* spp., *Valsa pini*, and *Therrya* spp. (Gierczyk et al. 2019) and root decay fungi, e.g., *Heterobasidion annosum* and *Rhizina undulata* (Tyburski et al. 2019). The higher temperature as a factor changing the plants' response to the pathogens is broadly discussed by Desaint et al. (2021). Pine trees growing beyond their natural range may be particularly susceptible to *C. ferruginosum* (Kowalski and Domański 1983; Kowalski 1997; Jurc et al. 2000). In Europe, this applies primarily to *Pinus nigra*, whose admixture in *Pinus sylvestris* stands may be the primary source of infection giving rise to damaging dieback of *P. sylvestris* shoots (Kowalski 1997; Jurc et al. 2000). The forests growing on quasi-natural stands and composed by native plants are much more resistant to the changes (Manion 1991; Sierota 2011; Jactel et al. 2017).

Phytopathogens and entomopathogens under drought

The lack of water in the soil stresses trees physiologically and stimulates the development of root pathogens. Kubiak et al. (2017) provide extensive literature describing the impact of drought and climate change on the pathogenesis of *Armillaria* spp. When discussing the impact of drought on tree-pathogen relationships, one should not ignore the

pests in the ‘*Spruce-Armillaria-Ips typographus*’ syndrome (Sierota and Grodzki 2020). It has been shown by Netherer et al. (2019) and Mezei et al. (2017) that drought and high temperature greatly weaken trees and influence bark beetle activity in spruce stands in the Austrian mountains. This phenomenon is also observed in Poland, particularly in the Białowieża Forest and in spruce stands in the Tatra Mountains. Favorable conditions for the aggregation of bark beetles last only a few days. The beetles receive a volatile signal secreted by a weakened tree (phenolic compounds, oleoresins) which is an impulse to aggregate the community (Lieutier 2002). The chemical compounds are emitted by mycelium both of *Armillaria* spp. (Lung-Escarmant and Guyon 2003), and members of Ophiostomatales associated with beetles (Jankowiak and Hilszczański 2005). Some authors show that volatile compounds of the decomposed phloem and wood, has a pheromonal effect on females (Krokene and Solheim 1997; Vega and Blackwell 2005). Referring to the Janzen-Connell -effect (Liang et al. 2015), it can be assumed that fungi and beetles play the role of selection factors for trees in the artificial ecosystem with excessive proportion of spruce, as observed in many commercial stands. However, it is observed that the influence of bark beetles is much less pronounced in natural stands.

The occurrence of *Pleurotus abieticola* has recently been observed as an indirect result of drought in Poland. This rare fungus appears on spruce trees several years after infestation of spruce bark beetles (Fig. 5b). This recent phenomenon seems connected with climate change because the sudden infection of spruce by this fungus was not previously documented, and the fungus is formerly known to occur on only a few sites in Poland (Kujawa et al. 2017; Gierczyk et al. 2018; Żółciak 2019). The sporocarps of many fungi known from their endophytic growth appear after water movement through xylem vessels stops (Boddy et al. 2017). An excellent example of fungal response for water deficiency is the presence of *Schizophyllum commune* fruitbodies, which occur along the entire length of the tree’ stem just after the tree death. *S. commune* is a wound parasite on living trees, e.g., after bark fire damage or old sunscorch. This fungus tolerates both heat and desiccation (Butin 1995; Schmidt 2006; Boddy and Heilmann-Clausen 2008; Takemoto et al. 2010).

Common ash (*Fraxinus excelsior*) is an important tree species in Europe, distributed from Iran to Ireland and from southern Scandinavia to northern Spain (Kárpáti 1970). In the Białowieża National Park in Poland, losses of ash trees have reached up to 75% (Miścicki 2016). The roots of *Fraxinus* species are predominantly colonized by arbuscular mycorrhizal (AM) fungi (Lyr et al. 1992; Weber and Claus 2000). Although the roots of AM tree species are less sensitive to drought than those of EM trees (Liese et al. 2019), mycorrhizal fungi cannot adequately protect *Fraxinus* from

the damage caused by rapidly developing fungi in the canopy what is eventually a reason for the ash-dieback.

As another indirect consequence of increasing drought on deciduous trees, pathogens such as members of the Ophiostomatales may be more vital during periods of tree stress (Pautasso et al. 2013), being lethal for individual trees or even entire stands (Jankowiak and Hilszczański 2005; Pandey et al. 2015; Terhonen et al. 2019). Although *Fraxinus* spp. are considered shade and waterlogging tolerant, remarkably high air temperatures and low humidity can activate some pathogens that appear on young regrowth such as *Diplodia mutila*, *Phomopsis* spp. and *Cytospora* spp. of weakened trees (Przybył 2002; Kowalski, Łukomska 2005, Kowalski 2007a, b). However, in the case of ash *F. excelsior* dieback in Europe, *Hymenoscyphus fraxineus* (syn. *Chalara fraxinea*) plays a leading role in pathogenesis. However, as several authors mention, high temperatures on the forest floor in summer are not conducive to growth and sporulation during the development of *H. fraxineus* ascospores (Ghelardini et al. 2017; Grosdidier et al. 2018; Hietala et al. 2018), but they may reappear in autumn after a period of high temperatures. The infection of shoots with the pathogen is less likely during prolonged dry periods, but the pathogen usually persists on pseudosclerotic petioles in some years (Kirisits 2015). The problem is still open, particularly since Díaz-Yáñez et al. (2020), in turn, question the influence of drought on ash development and survival.

Attention is also drawn to the growing problem of mistletoe in forests. *Viscum album* subsp. *austriacum* is observed in Scots pine stands in Poland, *V. album* subsp. *album* occurs on different deciduous trees or *V. album* subsp. *abietis* on fir (Plagnat 1950; Zuber 2004; Szmidla et al. 2019). This hemiparasite is indicated in Poland by crown thinning and death of Scots pine trees during drought, most often in older stands. The intense occurrence of mistletoe also limits the activity of mycorrhizal roots by a shortening carbohydrates supply from dying tree crowns, worsening its water balance and accelerating drought symptoms (Barbu 2010; Szmidla et al. 2019; Billigly et al. 2018; Skrypnik et al. 2020). Gehring and Whitham (1991) found a significant impact of Juniperus mistletoe (*Phoradendron juniperinum* Engelm.) on root mycorrhizal status and noted greater dieback of trees than those without mistletoe, despite growing under the influence of water and nutrient deficiency. Cullings et al. (2005) suggested that mistletoe in the tree canopy not only selects ectomycorrhizal species in tree roots, but also affects soil microbial activity and the local ecosystem. It is worthy adding that some pathogens of the *V. album* e.g., *Sphaeropsis visci*, which is a quite common species in Central Europe (Gierczyk et al. 2019; Tkaczyk and Sikora 2020), can be a natural barrier to mistletoe spreading. Chen et al. (2018) reports that this pathogen decreases the Asian mistletoe fitness.

The drought is a period of extensive activity of many plant consumers especially from Hymenoptera, Lepidoptera, and Homoptera orders. The insects protected by chitinous exoskeletons are less sensitive to insolation. Moreover, some insects and mites forage under the epidermis or inside plant tissues where they are protected from drying out. It seems that the influence of drought leads to an increase in herbivorous insect populations and disproportionate mortality of trees (Anderegg et al. 2015). Contrary, the period of drought is extremely unfavorable for some entomopathogens. Fungi of the order Entomophthorales, which are normally especially useful in insect regulation, are unable to adapt to water shortages and are practically absent in their active stage during dry seasons (Delalibera et al. 2000). The authors found that the humidity (RH) favorable for development of *Neozygites* spp.—parasite of mites feeding on cassava—is 70–79%, which means that during dry periods *Neozygites* spp. is observed only as dormant spores or hyphal bodies within dead individuals. The biological control of plant parasitic insects should be therefore during dry seasons focused rather on fungi belonging to Ophiocordycypitaceae and relatives (Lacey 2017).

The methods of counteracting changes in the population of fungi involved in interactions with plants

The protection of old-growth forest stands

During a deepening period of water deficit, the first trees to be affected are those that are not enough adapted to water stress, as well as those with inefficient ectomycorrhizal associates and trees already weakened by biotic factors and thus their removal should be treated as a factor of natural selection (Desprez-Loustau et al. 2006). The death of such trees increases access to light and moisture in the forest floor, which is undoubtedly beneficial for natural regeneration. However, prolonged droughts with high temperatures can lead to large-scale forest dieback. On fertile sites with abundant water, trees sparingly form ectomycorrhizal systems, or create endotrophic mycorrhizal systems, as in the case of ash or poplar (Danielson and Polle 2014). As a result, in the event of a water deficit in these habitats, such systems can be prone to damage due to dieback of mycorrhiza (Liu et al. 2015). The strong effects of drought are seen especially in stands planted during the post-war afforestation of former agricultural land in many countries of central Europe (former East Germany, Poland, Ukraine, Belarus, and Lithuania). In Poland, post-agricultural afforestation currently accounts for almost 2 million hectares of land, which is close to 22% of total forest area (Sierota et al. 2019). A characteristic feature of the soils in these afforested lands is

a shallow plow layer of soil previously cultivated for agriculture, completely different in physico-chemical and biotic structure than old forest soils, and the presence of a hard pan layer, sometimes containing high levels of iron and manganese (Smal and Olszewska 2008; Laganier et al. 2010). The hard pan hinders the development of taproots of many tree species (e.g., Scots pine, larch, birch and oak) and encourages the development of a shallow, horizontal root system. Such root systems mainly use water from the upper soil layer, rather than accessing moisture that is present deeper in the ground, and in conditions of low precipitation and high air temperatures they quickly dry out, heat up, and, in winter, freeze (Raitio 2000; Bakker et al. 2006; Gurskaya and Shiyatov 2006). This can lead to damage of mycorrhiza, as well as to structural changes in the roots themselves (Sutinen et al. 1996; Cleavitt et al. 2008), which promotes the development of root pathogens and causes shoot damage (Schoeneweiss 1981; Marcais and Breda 2006; Elad and Pertot 2014). According to the present forest policy (Bernadzki 1990; Hausler and Scherer-Lorenzen 2001; Brzeziecki 2008) and increasing role of natural regeneration in managed forests (Peterken 1999; Bürgi 2015), such man-made interventions—costly and against near-to-nature forestry—are rare. The protection of old-growth forests, the avoiding of clearcuttings, and the sustaining of biodiversity in the level of forest trees as well as of forests microbiota are the easiest way to avoid the strong drought damages.

Prevention of water drainage and afforestation policy with special interest on stress-tolerant trees

Forest stands may be adapted to avoid drought caused by climate change by preventing the outflow of water in streams and small rivers, which increases soil moisture in nearby stands. Such treatments should be preceded by detailed environmental assessments, as the risk of failure of such approaches can be high. Adaptation of stands to climate change may also be done by favoring regeneration by tree species more resistant to drought or those that consume less water. The number of such tree species that also produce commercially valuable wood on poor sandy soils is rather limited. The introduction of non-native species also carries risks (Thuiller et al. 2008; Lindner et al. 2010). The share of birch in a stand often indicates the possibility of lower soil moisture on the site. Bernadzki (1990) showed that soil moisture content under a birch stand is lower than under other tree species, which is explained by the strong transpiration by birch, drying the soil due to high rates of tree water uptake. Sandy mugwort soils show the lowest water holding capacity, both capillary and field; brown soils hold slightly higher amounts of water and black soils, and muds hold the greatest amount of water (Musierowicz and Król 1962). Birch, as a pioneer

species, occupies any above-mentioned soils, and even on infertile podzol soils it creates an extensive root system. The root system forms mycorrhizal associations, often with *Amanita muscaria*, *Lactarius pubescens*, *Paxillus involutus* or *Hebeloma crustuliniforme*. Therefore, mycorrhiza helps a tree occupying a poor habitat by improving water supply. The fungi in the next step can easily enter in contact with seedlings with other tree species. The presence of the rich, natural, or quasi-natural forests next to the new stand provides access to the spores of mycorrhizal fungi, which are disseminated by wind and animals. Forestry management should involve extending the existing forest complexes and creating green corridors rather than establishment of new separated stands. Adapting stands to drought can be achieved by eliminating inter- and intraspecific competition between trees and other vegetation for water (Parmesan 2006). Stand thinning can increase water availability for the remaining trees. However, eliminating competition by non-commercial forest vegetation, including many widespread non-commercial tree species in lowland coniferous forests, such as black cherry known also as American bird cherry (*Prunus serotina*) would be challenging (Horgan et al. 2003).

The stimulation of mycorrhization

Gehring et al. (2017) found that ectomycorrhizal community composition is under strong plant genetic control. The ECM communities should be therefore designed to the particular genotypes, or some artificially obtained tree clones easily entering in the symbiosis should be planted as necessary addition during afforestation practices. It was showed that the growth of artificially mycorrhized *Pinus sylvestris* seedlings with *Thelephora terrestris* inhabiting dry environments is much faster than non-mycorrhizal seedlings (Hilszczańska and Sierota 2006). This suggests that forests around the world with poor diversity of mycorrhizal association are more vulnerable to the warmer and drier climates predicted for the future (Pilosof et al. 2017). The artificial mycorrhization with using of media (ex. hemp seeds) containing the mycelium are rather not effective due to natural colonization of roots and artificial media by different fungi and bacteria. The planting of seedlings with developed mycorrhiza should give much better results. In pine European forests the mycorrhization using *Scleroderma citrinum*, and *Rhizopogon* spp. seems to be promising (Duñabeitia et al. 2004; Dučić et al. 2008).

Perspectives

The impact of the drought could be avoided using irrigation and rationing water for use in forests from water stored in catchments around forests. By using small water retention means, the natural retention capacity increases, which contributes to the potential for an increased amount of water that can be naturally stored and used in the forest. We are not able to regulate completely these processes, but the care of peatlands and bogs in the forests is one of the easiest ways to catch water in landscape and soil. The question for the forestry community is what can be done to reduce the effects of drought by improving the mycorrhizal status of trees? Since ectomycorrhizal fungal community composition ultimately determines the functionality of a fine-root system, the question seems to be fundamental. On the other hand, endophytes are a potential source of biological agents for controlling pests and diseases of seeds and mature plants. The growing interest in these organisms is heading toward their use in biological plant protection (e.g., Blumenstein et al. 2015; Terhonen et al. 2018; Verma and White 2019).

What is the possibility of adapting species composition, both of mycorrhizal and endophytic fungi as well as tree species, to water shortage? Is it possible to use mycorrhiza to help regenerate stands in drought prone, nutrient poor habitats, such as former agricultural land or formerly forested dune areas? The answer should be sought in local small retention, creation, and restoration of engineering structures with backwater devices (culvert-penstock, dike), adequate drainage in areas around the forest, or in the planting of trees with artificial and natural mycorrhization, as it is shown by Szabla and Pabian (2009).

It should be remembered that trees that currently are naturally producing seedlings to form future stands will themselves grow for several more decades and will be exposed to changes in climate much greater than have occurred to date. It is, therefore, necessary to consider mitigation, the reduction in greenhouse gas emissions, as well as adaptation, and to move away from petroleum products and replace them with natural renewable materials.

These challenges caused by climate change may lead to a change in the primary goal of forest management to that of being simply to maintain the natural functions of forests. Climate change may therefore force the development of entirely new models of forest management (Härkönen et al. 2019). Guy Ryder—UN-Water Chair at the 24th UN-Water Meeting in Geneva, 2016 stated that „*There is no life without water*”—but it is not the entire truth—“*There is no forest without fungi*” and any effort to improve forest conditions must take the state of the local mycobiota into account.

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Authors' contributions AB generated the meteorological field data; all authors substantially contributed to conceptualization, resources, writing the original draft, review and editing the text. ZS, DH and MW provided the general concept for the project.

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Declarations

Conflict of interest Authors declare no personal circumstances or interests that may be perceived as inappropriately influencing the representation or interpretation of reported research results.

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