

VPLIV SUŠE NA DROBNE KORENINE DREVES IN EKTOMIKORIZO V GOZDNIH EKOSISTEMIH

EFFECTS OF DROUGHT ON TREE FINE ROOTS AND ECTOMYCORRHIZA IN FOREST ECOSYSTEMS

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IZVLEČEK

Sušni stres sproži tako pri drobnih koreninah dreves kot pri ektomikoriznih glivah številne spremembe na različnih nivojih. Drevesa se branijo pred sušo z mehanizmi izogibanja in tolerance. Suša lahko vpliva na kolonizacijo z ektomikoriznimi glivami in na strukturo ektomikorizne združbe. Pomembno vlogo pri preživetju mladja ob suši imajo skupne micelijske mreže. Ob zmerni suši je kolonizacija z ektomikoriznimi glivami večja kot ob ekstremni suši, kar ima za drevo številne pozitivne učinke. V sušnih razmerah se pogosto še posebej poveča pogostnost ektomikorizne vrste *Cenococcum geophilum* Fr., ki omogoča, da drobne korenine ostanejo funkcionalne in takoj po končanem sušnem obdobju pričnejo z absorpcijo vode. V sušnih razmerah se poveča tvorba težko razgradljivih molekul v koreninah (lignin), prav tako pa se težko razgradljive molekule (melanin) tvorijo tudi pri ektomikorizni vrsti *C. geophilum*, kar prispeva h kopičenju težko razgradljivih organskih snovi v tleh.

Ključne besede: globalne spremembe, drobne korenine, mikorizne glive, prilagoditve, organska snov v tleh

ABSTRACT

Drought stress elicits many changes in tree fine roots and ectomycorrhizal fungi. Trees cope with drought through avoidance mechanisms or tolerance. Drought can result in changes in colonization by ectomycorrhizal fungi and in the structure of ectomycorrhizal communities. Survival of tree seedlings is supported through common mycelium networks. In moderate drought, there is greater colonization by ectomycorrhizal fungi compared to severe drought, resulting in several beneficial effects to the tree. Under drought, the frequency of ectomycorrhizal fungus *Cenococcum geophilum* Fr. often increases. *C. geophilum* sustains tree fine roots function and therefore roots are able to absorb water as soon as the drought period is over. Under drought, synthesis of recalcitrant organic compounds in roots, e.g. lignine, is increased. Recalcitrant compounds such as melanine are also found in *C. geophilum*, contributing to the accumulation of recalcitrant soil organic matter.

Key words: global changes, fine roots, mycorrhizal fungi, adaptation, soil organic matter

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1 UVOD

1 INTRODUCTION

V zadnjih desetletjih v nekaterih delih Evrope beležijo vse pogostejša sušna obdobja kot posledico naraščajočih temperatur (Briffa in sod., 2009; Hanel in sod., 2018). Pričakovati je, da se bo trend naraščanja temperatur in pogostosti ter intenzivnosti vročinskih valov v prihodnosti nadaljeval (Kirtman in sod., 2013; Vogel in sod., 2017), kar bo poleg neposrednega negativnega vpliva na vlažnost tal okrepilo negativne učinke morebitne manjše količine padavin. V prihodnosti naj bi se poleti povprečna količina padavin v Mediteranu in srednji Evropi zmanjšala, padavine pa naj bi se pogosteje pojavljale v obliki padavinskih ekstremov (Rajczak in Schär, 2017). Vlažnost površinskega sloja tal naj bi v južni Evropi upadala prek celega leta, poleti in jeseni pa tudi v osrednji in zahodni Evropi, medtem ko naj bi

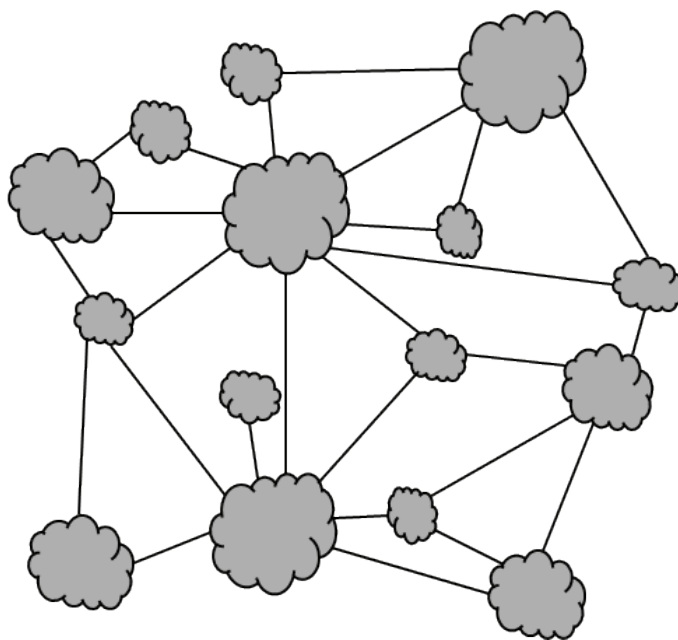
pogostnost zelo nizkih vrednosti talne vlage naraščala (Ruosteenoja in sod., 2018). Povratna zanka med vlažnostjo tal in temperaturo zraka dodatno krepitvaturne ekstreme (Vogel in sod., 2017). Nizka vlažnost tal zmanjšuje evapotranspiracijo ter tako povečuje toplotni tok, z njim pa pojavljanje višjih temperatur zraka, medtem ko visoke temperature zraka povečujejo deficit vlage v zraku, s čimer se evapotranspiracija nadaljuje kljub upadajoči vlažnosti tal (Ruosteenoja in sod., 2018). Navedene spremembe bodo imele močan vpliv na obstoječe gozdne ekosisteme in biogeokemijsko kroženje v njih. Naraščajoča pogostost ekstremnih vremenskih dogodkov bo prispevala k odmiranju gozdov in povzročila spremembe gozdnih združb zaradi večje občutljivosti drevesnega mladja na ekstremne vremenske dogodke (največji delež umrljivosti je pri mladju) ter zaradi povečanih obstoječih pritiskov na gozdove

v marginalnih okoljih (Pickles in Simard, 2017). Poleg same suše v toplejših in sušnejših razmerah gozdovom grozijo tudi pogostejši požari in napadi žuželk (Seidl in sod., 2017). Medtem ko je bilo opravljenih razmeroma veliko raziskav o vplivu globalnih sprememb na nadzemne dele najpogostejših evropskih drevesnih vrst, je vpliv na drevesne korenine in mikorizne glive, ki živijo v tesnem sožitju z drobnimi koreninami gozdnega drevja, precej neraziskan. Drobne korenine gozdnega drevja, ki jih običajno definiramo kot korenine, tanjše od 2 mm, dosejajo manj kot 2 % drevesne biomase v zmernih in borealnih gozdovih, vendar pa so nadvse aktiven del gozda, saj prek njih poteka absorpcija vode in hranil, s svojim hitrim obratom (angl. turnover rate) pa znatno prispevajo h kroženju ogljika v tleh (Brunner in Godbold, 2007).

Mikorizne glive so med ključnimi talnimi organizmi za delovanje gozdnih ekosistemov. V evropskih gozdovih zmernega pasu je večina sestojnih drevesnih vrst ektomikoriznih (Kraigher in sod., 2013). Pri ektomikorizni glivni plašč ovija drobne korenine, hife pa prodirajo med koreninskimi celicami v obliki mreže, ki jo imenujemo Hartigova mreža. Z izvenmatričnim micelijem, ki ga sestavljajo posamezne hife, ter rizomorfi, snopi hif, ki lahko vsebujejo specializirane strukture za transport vode in toplencev, ektomikorizna gliva sega tudi v okoliški substrat (Agerer, 2001) ter ustvarja velike skupne micelijske mreže (angl. common mycelial networks), ki povezujejo koreninske sisteme sosednjih ter tudi bolj oddaljenih dreves (Simard in Durall, 2004; Simard in sod., 2012). Skupne micelijske mreže pove-

zujejo več dreves iste vrste ali več različnih drevesnih in glivnih vrst. Velikost skupnih micelijskih mrež merimo v desetinah metrov, lahko pa ena sama gliva zajema območje velikosti več sto hektarov gozda. Velika stara drevesa, t.i. materinska drevesa, v skupnih micelijskih mrežah delujejo kot vozlišča (slika 1). Skupne micelijske mreže vplivajo na vzpostavitev drevesnega mladja, njihovo preživetje, rast, fiziologijo, zdravstveno stanje in kompeticijske sposobnosti. Prek skupnih micelijskih mrež poteka izmenjava virov (ogljik, voda, dušik, fosfor, mikronutrienti), stresnih molekul, alelokemikalij, s pomočjo skupnih micelijskih mrež pa se z ektomikoriznimi glivami kolonizira tudi mladje. Izmenjava virov poteka po principu gradienta vir-ponor. Stresni signali lahko po skupnih micelijskih mrežah potujejo zelo hitro, v roku nekaj ur (Gorzalak in sod., 2015). Morfološko lahko ektomikorizne glive glede na izhajajoče hife in rizomorfe razporedimo v različne eksploracijske tipe (npr. kontaktni eksploracijski tip, eksploracijski tip na kratke, srednje ali dolge razdalje, itd.), ki naj bi imeli v tleh različno funkcijo, razlikujejo pa se v tem, kako daleč v okoliški substrat segajo hife oz. rizomorfi (Agerer, 2001). Tako npr. lahko kontaktni eksploracijski tip, ki nima izhajajočih hif ter rizomorfov, privzema snovi samo prek plašča, ki je v neposrednem stiku z okoliškim substratom, medtem ko eksploracijski tip na dolge razdalje lahko privzema snovi iz okoliškega substrata tudi več decimetrov stran od koreninskega vršička, saj rizomorfi segajo tako daleč (Agerer, 2001).

Ektomikorizne glive zagotavljajo v gozdnih ekosistemih številne usluge s pomočjo morfoloških, fizio-



Slika 1: Shema povezav med drevesi prek skupnih micelijskih mrež. Večje oblike so starejša in večja drevesa. Starejša drevesa imajo vlogo vozlišč. Prilagojeno po Simard (2018).

Fig. 1: Connections between trees via common mycelial networks. Larger shapes represent older and larger trees. Older trees act as hubs. Adapted from Simard (2018).

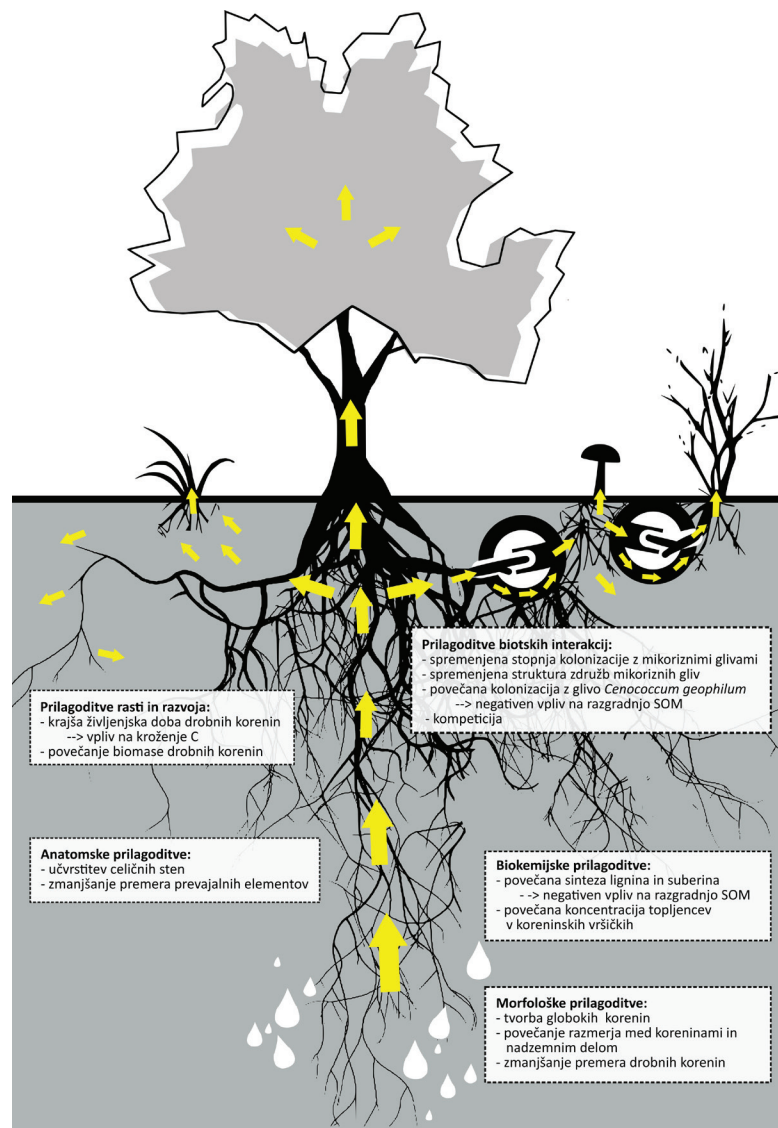
loških in ekoloških mehanizmov, kot so: kolonizacija večjega volumna tal, kolonizacija manjših por v tleh zaradi manjšega premera glivnih hif v primerjavi z drobnimi koreninami, povečana površina za absorpcijo hranil, sproščanje slabo dostopnih makrohranil, izločanje eksudatov, ki omogočajo večjo dostopnost mikrohranil, spreminjanje pH v mikorizosferi, prerazporejanje vode in hranil v prostoru in času ter vzpostavljanje povezav med viri in ponori ogljika (Kraigher in sod., 2013). Če želimo z večjo natančnostjo predvideti odziv gozdnih ekosistemov na okoljske spremembe v prihodnosti, moramo poznati tudi odziv drobnih korenin v povezavi z mikoriznimi glivami (Staddon in sod., 2003).

2 VPLIV SUŠE NA DROBNE KORENINE DREVES

2 EFFECTS OF DROUGHT ON TREE FINE ROOTS

Rastlinam dostop do omejenih virov v tleh omogočajo različne strategije, ki jih lahko razdelimo v pet

skupin: arhitekturne (razraščanje koreninskega sistema, globina koreninjenja), morfološke (premer korenin, specifična dolžina korenin), fiziološke (kinetika privzema hranil, respiracija, izločanje eksudatov) in biotske (interakcije s simbiotskimi in drugimi organizmi) (Bardgett in sod., 2014). Variabilnost v značilnostih koreninskega sistema (angl. root traits) je velika tako med vrstami kot tudi med genotipi, poleg tega pa je koreninski sistem izredno plastičen, kar omogoča, da se rastlina prilagaja spremenljivim razmeram v okolju, še posebej kar se tiče dostopa do hranil in vode (Bardgett in sod., 2014). Posamezni deli koreninskega sistema se pojavljajo v slojih oz. delih tal z različno vlažnostjo, pri čemer prihaja do pasivnega gibanja vode prek korenin iz vlažnejših proti sušnim delom tal, kar imenujemo hidravlična distribucija (slika 2). Ko se listne reže zaprejo in je transpiracija majhna, se vodni potencial rastline poskuša izenačiti z vodnim potenci-



Slika 2: Shema hidravlične redistribucije vode v tleh s pomočjo drevesnih korenin (rumene puščice) ter povzetek prilagoditev korenin na sušo (pripravila D. Finžgar in T. Mrak).

Fig. 2: Hydraulic redistribution of soil water by tree roots (yellow arrows) and summary of adaptation of roots to drought (prepared by D. Finžgar & T. Mrak).

alom tal, v katerih je najaktivnejši del korenin, zato se tla navlažijo. Najbolj poznan tip hidravlične redistribucije je hidravlični dvig, do katerega pride, kadar so globlji deli tal vlažnejši kot površinski (Prieto in sod., 2012). Hidravlični dvig je možen le pri rastlinah, ki so sposobne tvorbe globokega koreninskega sistema, vendar pa imajo od njega lahko koristi tudi sosednje rastline s plitvejšim koreninskim sistemom, npr. kombinacija gradna (*Quercus petraea* (Matt.) Liebl.) in bukve (*Fagus sylvatica* L.) (Pretzsch in sod., 2013), bodisi neposredno s privzemom vode, ki jo rastlina z globokim koreninskim sistemom sprošča v okolico, bodisi posredno prek mikoriznih gliv (Prieto in sod., 2012).

V mešanih sestojih lahko prihaja v sušnih razmerah do kompeticije med drobnimi koreninami. V mešanih sestojih bukve in navadne smreke (*Picea abies* (L.) Karst) so drobne korenine smreke še bližje površju tal kot v čistih sestojih smreke, kjer so potencialno bolj izpostavljene poletni suši, poleg tega pa so manj razvejene ter imajo manjši delež simbioze z eksploracijskimi tipi ektomikoriznih gliv na dolge razdalje. Vendar pa je učinek prisotnosti bukve na dostopnost vode za smreko po drugi strani v času spomladanske suše pozitiven, saj je v mešanih sestojih bukve in smreke zaradi listopadnosti bukve kompeticija za vodo manjša kot v čistih sestojih smreke. Kompeticiji so izpostavljene samo smreke, ki so v neposredni sosesčini bukve, kar pomeni, da je v mešanem gozdu z vidika suše pojavljanje smrek v skupinah bolj ugodno od pojavljanja posameznih smrek (Goisser in sod., 2016).

Tako kot nadzemni deli, se tudi korenine odzivajo na stresne razmere suše po načelu dveh strategij - izogibanja in tolerance. Pri izogibanju suši gre za usklajevanje vodnega statusa nadzemnega in podzemnega dela, lovljenje ravnotežja med izgubo vode in njenim privzemom. Kratkoročno se drevo izogiba pretirani izgubi vode z zapiranjem listnih rež, dolgoročno pa z zmanjšano rastjo nadzemnega dela, ki vodi v povečanje razmerja med koreninami in nadzemnim delom. Privzem vode v korenine se lahko izboljša s tvorbo večjega števila drobnih korenin ter tvorbo globokih korenin, ki iščejo vire vode (Brunner in sod., 2015).

Mehanizmi tolerance omogočajo neprekinjen transport vode, izmenjavo plinov in preživetje celic pri majhnih vodnih potencialih, kar drevo doseže s prilagoditvijo ozmotskega potenciala v koreninah s kopičenjem topljencev, s povečanjem odpornosti na kavitacijo z učvrstitvijo celičnih sten prevodnih tkiv ter z zmanjšanjem premera ksilemskih prevodnih elementov, ter s sposobnostjo celic, še posebej meristemskih, da ostanejo žive (Vilagrosa in sod., 2012; Brunner in sod., 2015). Korenine so bolj občutljive za kavitacijo

kot deblo, tako pri listavcih kot pri iglavcih, še posebej pa so kavitaciji izpostavljene tanjše korenine. Drevesa iste vrste, ki rastejo v sušnejših razmerah, so bolj odporna proti kavitaciji kot drevesa, ki rastejo v razmerah, kjer je vlage ves čas dovolj. V ekstremnih sušnih razmerah naj bi bila popolna kavitacija v tanjših koreninah zaščitni mehanizem, ki drevo hidravlično izolira od vedno bolj suhih okoliških tal. Dokler ostajajo listne reže zaprte, se tako prepreči, da bi v deblu nastal tako nizek tlak, da bi prišlo v njem do popolne kavitacije. Po končanem obdobju suše se vzpostavi nova rast korenin, tako da se hidravlična prevodnost zopet poveča, kavitirane prevodne poti pa se zapolnijo (Sperry in Ikeda, 1997). Pod vplivom suše se zmanjša pojavljanje lenticel v olesenelih drobnih koreninah, medtem ko je njen vpliv na pojavljanje branik v olesenelih drobnih koreninah različen med vrstami. Pri črničevju (*Quercus ilex* L.) se je pojavljanje branik v olesenelih drobnih koreninah debeline 2 mm zmanjšalo, pri dobu (*Quercus robur* L.) pa povečalo (Mrak in sod., 2019).

V drobnih koreninah sadik različnih provenienc bukve je suša povzročila upad količine ogljika, medtem ko je pri nekaterih proveniencah povzročila povečanje količine dušika, pri drugih pa ni bilo sprememb. Posledično se je pri vseh proveniencah zmanjšalo razmerje med C in N v drobnih koreninah (Dounavi in sod., 2016).

Življenjska doba drobnih korenin se v sušnih razmerah skrajša, razen takrat, kadar prihaja do hidravlične redistribucije vlage iz delov tal z večjo vlažnostjo v dele tal z manjšo vlažnostjo (McCormack in Guo, 2014). Poleg tega se zmanjša biomasa drobnih korenin, njihova dolžina ter frekvenca koreninskih vršičkov, na nekatere druge parametre, kot je specifična dolžina korenin, gostota koreninskega tkiva ter indeks koreninske površine, pa naj suša ne bi imela vpliva. Vendar na te rezultate vpliva odločitev, katere debelinske razrede vključiti v definicijo drobnih korenin. Raziskovalci, ki so mejo postavili pri 0,5 mm, namesto pri 2 mm, so v primeru suše ugotovili povečano biomaso drobnih korenin, njihova specifična dolžina je bila povečana, prav tako tudi gostota koreninskega tkiva, povprečni premer ter vsebnost dušika pa sta se zmanjšala (Brunner in sod., 2015). V sadikah doba (*Q. robur*) se je delež najtanjših korenin (debelinski razred 0,0–0,1 mm) pod vplivom suše značilno povečal, medtem ko se je delež debelejših drobnih korenin zmanjšal. Pri isti vrsti se je povprečna debelina drobnih korenin zmanjšala za 8,49 % (Mrak in sod., 2019). Pri črničevju (*Q. ilex*) so drobne korenine, ki zrastejo v suhem mediteranskem poletju, tanjše (Montagnoli in sod., 2019).

V sušnih razmerah se v koreninah sproži sinteza povečanih količin suberina in lignina. Suberin je v endo-

dermu in eksodermu korenin ter v peridermu sekundarno odebeljenih korenin. Suberinizacija zmanjšuje izgubo vode iz korenin, še posebej v sušnih razmerah, in izboljšuje učinkovitost izrabe vode. Z lignifikacijo celičnih sten se poveča njihova mehanska odpornost ter zmanjša izguba vode iz celic ter njihova dehidracija. Zaradi povečanih količin suberina in lignina v koreninah pride ob suši do sprememb v količini in razgradnji odmrle organske snovi v tleh ter s tem do sprememb v hitrosti obrata organske snovi v tleh. Zaradi suberina organska snov v tleh postane hidrofobna, lignin pa so sposobni razgrajevati le nekateri mikroorganizmi v tleh – glive rjave trohnobe in aktinobakterije, kjer pa lahko pride do vpliva suše na (encimsko) aktivnost teh mikroorganizmov. Poleg tega je za razgradnjo lignina v tleh ključno tudi razmerje med količino lignina in dušika (Brunner in sod., 2015).

3 VPLIV SUŠE NA SIMBIOZO Z EKTOMIKORIZNIMI GLIVAMI

3 EFFECTS OF DROUGHT ON SYMBIOSIS WITH ECTOMYCORRHIZAL FUNGI

S pomočjo ektramatričnega micelija se lahko voda prenaša od rastlin z dostopom do vira vode v globljih plasteh tal do rastlin, ki jim vode primanjkuje (Egerton-Warburton in sod., 2007). Ta način oskrbe z vodo je zelo pomemben za preživetje drevesnega mladja (Lehto in Zwiazek, 2011). V sušnih gozdovih je dostop do micelijskih mrež materinskih dreves ključen za vzpostavitev mladja. Mladje, ki raste znotraj micelijskih mrež materinskih dreves, je večje in bolj učinkovito pri izrabi vode. Združba ektomikoriznih gliv pri mladju je zelo podobna kot pri sosednjih odraslih drevesih. Povezava v micelijske mreže odraslih dreves mora nastopiti še pred pričetkom sušnega obdobja, zato imajo tu prednost lokalne, suši prilagojene provenience, ki kalijo zgodaj in se hitro povežejo v micelijske mreže odraslih dreves (Pickles in Simard, 2017). Izbira provenience ter način ravnanja s sadikami je v razmerah, kjer pričakujemo hude suše, bolj pomembna kot zanašanje na podporo skupnih micelijskih mrež. Sadike iste provenience, vzgojene v drevesnicah, imajo v takih razmerah prednost pred naravno regeneracijo iz semen (Bingham in Simard, 2013). Micelij, ki ima dostop do vira vode, lahko preživi v zelo suhih tleh (do -2,5 MPa vodnega potenciala tal ali celo manj). Hife so funkcionalno aktivne celo po 68–77 dneh suše in sposobne rasti po 70–80 dneh suše. Pri transportu vode na daljše razdalje igrajo glavno vlogo rizomorfi, ki omogočajo transport vode po simplastu (Querejeta in sod., 2003). Rizomorfe tvorijo glive s hidrofobnimi celičnimi stenami, glive s hidrofilnimi stenami pa tran-

sportirajo vodo po apoplastu. Zelo malo je znanega o tem, ali obstaja kakšna povezava med lastnostmi celičnih sten mikoriznih gliv ter njihovo odpornostjo proti suši (Lehto in Zwiazek, 2011). Ko so primerjali eksplozijske tipe ektomikoriznih gliv v sestoji obmorskega bora (*Pinus pinaster* Aiton) v vlažnejših in bolj sušnih razmerah, so ugotovili, da so eksplozijski tipi na dolge in kratke razdalje značilno bolj pogosti v sušnih tleh, kontaktni eksplozijski tipi pa v vlažnejših razmerah. Pogostnost eksplozijskih tipov na srednje razdalje je bila približno enaka (Bakker in sod., 2006). Pickles in Simard (2017) navajata, da ob suši pri mladju postanejo pogostejši tipi na srednje (*Amphinema*, *Boletus*, *Cortinarius*, *Tomentella*, *Tricholoma*) in dolge razdalje (*Rhizopogon*, *Suillus*).

Ugotovitve o vplivih suše na kolonizacijo z ektomikoriznimi glivami ter strukturo glivne združbe so zelo različne, kar lahko pripišemo razlikam v poskusnih razmerah (npr. trajanje suše in njena intenziteta) ter razlikam v izbranih ektomikoriznih inokulih v primeru uporabe inokuliranih sadik. Globalno naj bi bila kolonizacija z ektomikoriznimi glivami manjša v okoljih, kjer zasledimo veliko sezonskost padavin (Soudzilovskaia in sod., 2015). V naravnih razmerah naj bi kolonizacija z ektomikoriznimi glivami sledila hipotezi zmernega stresa gostiteljske rastline, z večjo stopnjo kolonizacije v razmerah zmernega stresa ter manjše v razmerah kroničnega stresa. Manjša kolonizacija z ektomikoriznimi glivami v razmerah hude suše, ko je stopnja fotosinteze majhna, pomaga pri ohranjanju omejenih zalog ogljika, ki bi jih rastlina sicer namenila glivi v zameno za hranila, za preživetje rastline (Swaty in sod., 2004). V sestojih hrasta vrste *Quercus agrifolia* Née, ki jih je prizadela večletna suša, je bila kolonizacija z ektomikoriznimi glivami zmanjšana (Querejeta in sod., 2003). Primerjava sestojev bora vrste *Pinus muricata* D. Don v razmerah 7-odstotne in 13-odstotne talne vlage je pokazala, da je kolonizacija večja v razmerah 13-odstotne talne vlage (Kennedy in Peay, 2007). Po drugi strani pa zmerna suša ni vplivala na kolonizacijo pri sadikah bukve (*Fagus sylvatica* L.) z naravno obstoječo mikorizo (Shi in sod., 2002) ter pri sadikah bukve, inokuliranih s petimi vrstami mikoriznih gliv (Pena in Polle, 2014). Kolonizacija se tudi ni spremenila v sušnem poskusu na sadikah hrasta, prav tako ni bilo značilnega vpliva na vrstno pestrost (Mrak in sod., 2019). Po drugi strani pa lahko na vrstno pestrost vpliva genotip rastline. Vrstna pestrost pri genotipu bora (*Pinus edulis* Engelm.), odpornega proti suši, je bila dvakrat večja kot pri genotipu, občutljivem za sušo. V primeru, ko sta bila oba genotipa izpostavljena sušnim razmeram, se je struktura ektomikorizne glivne združbe pri genotipu, občutlji-

vem za sušo, spremenila, pri genotipu, odpornem proti suši, pa ne (Patterson in sod., 2019).

Pogosto ob suši pride do sprememb v pogostnosti nekaterih vrst ektomikoriznih gliv (Shi in sod., 2002; Swaty in sod., 2004; Herzog in sod., 2013; Pena in Polle, 2014; Mrak in sod., 2019), npr. pogostnost ektomikoriznih gliv iz rodu *Tomentella* je ob suši upadla pri genotipu bora, občutljivega za sušo (Patterson in sod., 2019), prav tako pa je njihova pogostnost upadla pri sadikah hrastov, izpostavljenih suši, narasla pa je pogostnost vrste *Sphaerosporella brunnea* (Alb. & Schwein.) Svrcek & Kubicka ter vrste iz rodu *Thelephora* (Mrak in sod., 2019). Sprememba strukture glivne združbe proti na sušo odpornim ektomikoriznim glivam (oz. glivam, ki se zadovoljijo z zelo omejenim dotokom ogljika) bi bila za gostiteljsko rastlino ugodna/koristna, saj bi gliva rastlini potencialno še naprej zagotavljala različne usluge. V stresnih razmerah je privzem makrohranil (N in P) v rastlino moten, ektomikorizne glive pa lahko to omejitev vsaj v določeni meri odstranijo.

V laboratorijskih razmerah so ugotovili, da se mikorizna vrsta *Cenococcum geophilum* Fr. (slika 3) na sušni stres odziva v manjši meri kot druge mikorizne glive (Jany in sod., 2003; di Pietro in sod., 2007). Ta vrsta zagotavlja, da mikorizirane drobne korenine ostajajo funkcionalne, kar omogoča takojšen odziv na vir vode po končanem sušnem obdobju (Jany in sod., 2003). Povečano kolonizacijo z vrsto *C. geophilum* so pogosto zasledili v različnih stresnih razmerah, vključno s sušo (Bakker in sod., 2006; Grebenc in Kraigher, 2007; Kraigher in sod., 2007; Kraigher in sod., 2011). Pod

vplivom suše se regulacija dveh tipov akvaporinov pri tej vrsti glive v ektomikorizi spremeni, vendar pa raziskovalcem za zdaj značilne pozitivne povezave med fiziološkimi parametri drevesne vrste in mikorizacije z glivo *C. geophilum* še ni uspelo dokazati (Peter in sod., 2016). Pogostnost te vrste naj bi se povečala tudi v razmerah povišanih temperatur zraka in naj bi bila v pozitivni korelaciji z rastjo nadzemnega dela (Herzog in sod., 2013). Ker so hife vrste *C. geophilum* melanizirane, so po odmrtnju zelo odporne proti razgradnji v tleh, saj je melanin kompleksen polimer. Kopičenje melaniziranih ostankov v tleh zaradi nezmožnosti razgradnje prispeva k povečanju količine organske snovi v tleh (SOM). Na zmožnost razgradnje melaniziranih ostankov močno vpliva tudi razmerje med količino melanina in dušika, podobno kot v primeru korenin med količino lignina in dušika (Fernandez in Koide, 2014).

Encimska aktivnost ektomikorize, ki je povezana s sproščanjem C, N in P iz kompleksnih organskih molekul v tleh, je večja kot pri nemikoriznih koreninah, in ostane povečana kljub omejenemu dostopu do vode. Zelo je odvisna od vrste ektomikorizne glive in upada po naslednjem vrstnem redu: *Suillus granulatus* (L.) Roussel > *Rhizopogon roseolus* (Corda) Th. Fr. > *Paxillus involutus* (Batsch) Fr. > *C. geophilum* (Kipfer in sod., 2012). Oskrba z N v obliki NH_4^+ , ki jo vrsta *C. geophilum* zagotavlja v razmerah suše, je zelo majhna v primerjavi z drugimi ektomikoriznimi vrstami. Sposobnost za privzem N iz suhih tal naj bi bila povezana tudi z drugimi okoljskimi parametri (npr. osončenost) (Pena in Polle, 2014). Za vrsto *C. geophilum* so ugotovili tudi, da se en-



Slika 3: Ektomikorizna gliva *Cenococcum geophilum* Fr.

Fig. 3: Ectomycorrhizal fungus *Cenococcum geophilum* Fr.

cimska aktivnost poveča le v kombinaciji suše s povišanimi temperaturami, zelo pa naj bi bila odvisna tudi od vrste gostiteljske rastline (Herzog in sod., 2013).

Z vidika rastline imajo ektomikorizne glive v sušnih razmerah veliko pozitivnih učinkov. Izboljša se vodni potencial rastline, ohranja se hidravlična prevodnost, fotosinteza je večja kot pri nemikoriznih sadikah, zmanjšani so negativni učinki suše na rast podzemnih in nadzemnih delov, struktura lesa je manj prizadeta, smrt koreninskih vršičkov zakasnjena, vsebnost P v listih manj zmanjšana ter oksidativni stres manjši (Ortega in sod., 2004; Walker in sod., 2004; Alvarez in sod., 2009a; Alvarez in sod., 2009b; Kipfer in sod., 2010; Beniwal in sod., 2010; Danielsen in Polle, 2014). V sušnih razmerah se lahko poveča ozmotski potencial mikoriznih vršičkov zaradi kopičenja topnih sladkorjev in sladkornih alkoholov – poliolov (produkti gliv) z namenom ohranjanja privzema vode (Shi in sod., 2002).

4 SKLEPI

4 CONCLUSIONS

Drevesa imajo zelo plastičen koreninski sistem, kar omogoča različne prilagoditve na sušne razmere. Prilagoditve se kažejo na področju rasti in razvoja korenin, morfologije, anatomskih in biokemijskih lastnosti ter biotskih interakcij (slika 2). Kljub temu, da so glavni mehanizmi prilagoditev poznani, ostaja na tem področju še veliko neznank, sploh na področju biotskih in abiotskih interakcij, kar onemogoča takojšnji prenos teoretičnih znanj v načrtovanje gojenja gozdov. Zaradi klimatskih sprememb v smeri toplejših in sušnejših razmer bo najbolj na udaru drevesno mladje, ki še nima razvitega obsežnega koreninskega sistema. Čeprav lahko odrasla drevesa prek skupnih micelijskih mrež podpirajo obstoj mladja, bo v primeru pričakovanih hudih suš zelo pomembna izbira ustreznih provenienc sadik.

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6 VIRI

6 REFERENCES

- Agerer R. 2001. Exploration types of ectomycorrhizae. *Mycorrhiza*, 11, 2: 107–114.
- Alvarez M., Huygens D., Fernandez C., Gacitúa Y., Olivares E. in sod. 2009a. Effect of ectomycorrhizal colonization and drought on reactive oxygen species metabolism of *Nothofagus dombeyi* roots. *Tree Physiology*, 29, 8: 1047–1057.
- Alvarez M., Huygens D., Olivares E., Saavedra I., Alberdi M. in sod. 2009b. Ectomycorrhizal fungi enhance nitrogen and phosphorus nutrition of *Nothofagus dombeyi* under drought conditions by regulating assimilative enzyme activities. *Physiologia Plantarum*, 136, 4: 426–436.
- Bakker M.R., Augusto L., Achat D.L. 2006. Fine root distribution of trees and understory in mature stands of maritime pine (*Pinus pinaster*) on dry and humid sites. *Plant and Soil*, 286, 1–2: 37–51.
- Bardgett R.D., Mommer L., De Vries F.T. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, 29, 12: 692–699.
- Beniwal R.S., Langenfeld-Heyser R., Polle A. 2010. Ectomycorrhiza and hydrogel protect hybrid poplar from water deficit and unravel plastic responses of xylem anatomy. *Environmental and Experimental Botany*, 69, 2: 189–197.
- Bingham M.A., Simard S.W. 2013. Seedling genetics and life history outweigh mycorrhizal network potential to improve conifer regeneration under drought. *Forest Ecology and Management*, 287: 132–139.
- Briffa K.R., van der Schrier G., Jones P.D. 2009. Wet and dry summers in Europe since 1750: evidence of increasing drought. *International Journal of Climatology*, 29, 13: 1894–1905.
- Brunner I., Godbold D.L. 2007. Tree roots in a changing world. *Journal of Forest Research*, 12, 2: 78–82.
- Brunner I., Herzog C., Dawes M., Arend M., Sperisen C. 2015. How tree roots respond to drought. *Frontiers in Plant Science*, 6: 1–16.
- Danielsen L., Polle A. 2014. Poplar nutrition under drought as affected by ectomycorrhizal colonization. *Environmental and Experimental Botany*, 108: 89–98.
- di Pietro M., Churin J.L., Garbaye J. 2007. Differential ability of ectomycorrhizas to survive drying. *Mycorrhiza*, 17, 6: 547–550.
- Dounavi A., Netzer F., Čelepirović N., Ivanković M., Burger J. in sod. 2016. Genetic and physiological differences of European beech provenances (*F. sylvatica* L.) exposed to drought stress. *Forest Ecology and Management*, 361: 226–236.
- Egerton-Warburton L.M., Querejeta J.I., Allen M.F. 2007. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *Journal of Experimental Botany*, 58, 6: 1473–1483.
- Fernandez C.W., Koide R.T. 2014. Initial melanin and nitrogen concentrations control the decomposition of ectomycorrhizal fungal litter. *Soil Biology and Biochemistry*, 77, 150–157.
- Goisser M., Geppert U., Rötzer T., Paya A., Huber A. in sod. 2016. Does belowground interaction with *Fagus sylvatica* increase drought susceptibility of photosynthesis and stem growth in *Picea abies*? *Forest Ecology and Management*, 375: 268–278.
- Gozelak M.A., Asay A.K., Pickles B.J., Simard S.W. 2015. Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB PLANTS*, 7: plv050.
- Grebenc T., Kraigher H. 2007. Changes in the community of ectomycorrhizal fungi and increased fine root number under adult beech trees chronically fumigated with double ambient ozone concentration. *Plant Biology*, 9, 2: 279–287.
- Hanel M., Rakovec O., Markonis Y., Máca P., Samaniego L. in sod. 2018. Revisiting the recent European droughts from a long-term perspective. *Scientific Reports*, 8, 1: 9499.
- Herzog C., Peter M., Pritsch K., Günthardt-Goerg M.S., Egli S. 2013. Drought and air warming affects abundance and exoenzyme profiles of *Cenococcum geophilum* associated with *Quercus robur*, *Q. petraea* and *Q. pubescens*. *Plant Biology*, 15, 230–237.
- Jany J.L., Martin F., Garbaye J. 2003. Respiration activity of ectomycorrhizas from *Cenococcum geophilum* and *Lactarius* sp. in relation to soil water potential in five beech forests. *Plant and Soil*, 255, 2: 487–494.

- Kennedy P., Peay K. 2007. Different soil moisture conditions change the outcome of the ectomycorrhizal symbiosis between *Rhizopogon* species and *Pinus muricata*. *Plant and Soil*, 291, 1–2: 155–165.
- Kipfer T., Egli S., Ghazoul J., Moser B., Wohlgemuth T. 2010. Susceptibility of ectomycorrhizal fungi to soil heating. *Fungal Biology*, 114, 5–6: 467–472.
- Kipfer T., Wohlgemuth T., van der Heijden M.G.A., Ghazoul J., Egli S. 2012. Growth response of drought-stressed *Pinus sylvestris* seedlings to single- and multi-species inoculation with ectomycorrhizal fungi. *PLoS ONE*, 7, 4: e35275.
- Kirtman B., Power S.B., Adedoyin J.A., Boer G.J., Bojariu R. in sod. 2013. Near-term climate change: Projections and predictability. V: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Stocker T.F., Qin D., Plattner G.-K., Tignor M., Allen S.K., Boschung J., Nauels A., Xia Y., Bex V., Midgley P.M. (ur.). Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press: 953–1028.
- Kraigher H., Al Sayegh-Petkovšek S. 2011. Mycobioindication of stress in forest ecosystems. V: Rai M., Varma A. (ur.). *Diversity and biotechnology of ectomycorrhizae*. Soil biology, vol. 25. Heidelberg, New York, Springer: 301–322.
- Kraigher H., Al Sayegh-Petkovšek S., Grebenc T., Simončič P. 2007. Types of ectomycorrhiza as pollution stress indicators: case studies in Slovenia. *Environmental Monitoring and Assessment* 128, 1: 31–45.
- Kraigher H., Bajc M., Grebenc T. 2013. Chapter 8 - Mycorrhizosphere Complexity. V: *Developments in Environmental Science*. Matyssek R., Clarke N., Cudlin P., Mikkelsen T.N., Tuovinen J.P., Wieser G., Paoletti E. (ur.). *Developments in Environmental Science*, Elsevier: 151–177.
- Lehto T., Zwiazek J.J. 2011. Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza*, 21, 2: 71–90.
- McCormack M.L., Guo D. 2014. Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science*, 5: 1–11.
- Montagnoli A., Dumroese R.K., Terzaghi M., Onelli E., Scippa G.S., Chiatante D. 2019. Seasonality of fine root dynamics and activity of root and shoot vascular cambium in a *Quercus ilex* L. forest (Italy). *Forest Ecology and Management*, 431: 26–34.
- Mrak T., Štraus I., Grebenc T., Gričar J., Hoshika Y., Carriero G., Paoletti E., Kraigher H. 2019. Different belowground responses to elevated ozone and soil water deficit in three European oak species (*Quercus ilex*, *Q. pubescens* and *Q. robur*). *Science of the Total Environment*, 651: 1310–1320.
- Ortega U., Duñabeitia M., Menendez S., Gonzalez-Murua C., Majada J. 2004. Effectiveness of mycorrhizal inoculation in the nursery on growth and water relations of *Pinus radiata* in different water regimes. *Tree Physiology*, 24, 1: 65–73.
- Patterson A., Flores-Rentería L., Whipple A., Whitham T., Gehring C. 2019. Common garden experiments disentangle plant genetic and environmental contributions to ectomycorrhizal fungal community structure. *New Phytologist*, 221: 493–502.
- Pena R., Polle A. 2014. Attributing functions to ectomycorrhizal fungal identities in assemblages for nitrogen acquisition under stress. *Isme Journal*, 8, 2: 321–330.
- Peter M., Kohler A., Ohm R.A., Kuo A., Krützmann J. in sod. 2016. Ectomycorrhizal ecology is imprinted in the genome of the dominant symbiotic fungus *Cenococcum geophilum*. *Nature Communications*, 7: 12662.
- Pickles B.J., Simard S.W. 2017. Chapter 18 - Mycorrhizal networks and forest resilience to drought. V: *Mycorrhizal mediation of soil*. Johnson N.C., Gehring C., Jansa J. (ur.). Elsevier: 319–339.
- Pretzsch H., Schütze G., Uhl E. 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology*, 15: 483–495.
- Prieto I., Armas C. Pugnaire F.I. 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytologist*, 193, 4: 830–841.
- Querejeta J., Egerton-Warburton L., Allen M. 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia*, 134, 1: 55–64.
- Rajczak J., Schär C. 2017. Projections of future precipitation extremes over Europe: A multimodel assessment of climate simulations. *Journal of Geophysical Research: Atmospheres*, 122, 20: 10773–10800.
- Ruosteenoja K., Markkanen T., Venäläinen A., Räisänen P., Peltola H. 2018. Seasonal soil moisture and drought occurrence in Europe in CMIP5 projections for the 21st century. *Climate Dynamics*, 50, 3: 1177–1192.
- Seidl R., Thom D., Kautz M., Martin-Benito D., Peltoniemi M. in sod. 2017. Forest disturbances under climate change. *Nature Climate Change*, 7: 395.
- Shi L.B., Guttenberger M., Kottke I., Hampp R. 2002. The effect of drought on mycorrhizas of beech (*Fagus sylvatica* L.): changes in community structure, and the content of carbohydrates and nitrogen storage bodies of the fungi. *Mycorrhiza*, 12, 6: 303–311.
- Simard S.W. 2018. Mycorrhizal networks facilitate tree communication, learning, and memory. V: *Memory and learning in plants. Signaling and communication in plants*. Baluska F., Gagliano M., Witzany G. (ur.). Cham, Springer: 191–213.
- Simard S.W., Beiler K.J., Bingham M.A., Deslippe J.R., Philip L.J. in sod. 2012. Mycorrhizal networks: Mechanisms, ecology and modeling. *Fungal Biology Reviews*, 26, 1: 39–60.
- Simard S.W., Durall D.M. 2004. Mycorrhizal networks: a review of their extent, function, and importance. *Canadian Journal of Botany*, 82, 8: 1140–1165.
- Soudzilovskaia N.A., Douma J.C., Akhmetzhanova A.A., Bodegom P.M., Cornwell W.K. in sod. 2015. Global patterns of plant root mycorrhizal colonization intensity. *Global Ecology and Biogeography*, 24: 371–382.
- Sperry J.S., Ikeda T. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology*, 17: 275–280.
- Staddon P.L., Thompson K., Jakobsen I., Grime J.P., Askew A.P. in sod. 2003. Mycorrhizal fungal abundance is affected by long-term climatic manipulations in the field. *Global Change Biology*, 9, 2: 186–194.
- Swaty R.L., Deckert R.J., Whitham T.G., Gehring C.A. 2004. Ectomycorrhizal abundance and community composition shifts with drought: Predictions from tree rings. *Ecology*, 85, 4: 1072–1084.
- Vilagrosa A., Chirino E., Peguero-Pina J.J., Barigah T.S., Cochard H. in sod. 2012. Xylem cavitation and embolism in plants living in water-limited ecosystems. V: *Plant Responses to Drought Stress*. Aroca R. (ur.). Berlin, Heidelberg, Springer: 63–109.
- Vogel M.M., Orth R., Cheruy F., Hagemann S., Lorenz R. in sod. 2017. Regional amplification of projected changes in extreme temperatures strongly controlled by soil moisture-temperature feedbacks. *Geophysical Research Letters*, 44, 3: 1511–1519.
- Walker R.F., McLaughlin S.B., West D.C. 2004. Establishment of sweet birch on surface mine spoil as influenced by mycorrhizal inoculation and fertility. *Restoration Ecology*, 12, 1: 8–19.

1 INTRODUCTION

The frequency of summer drought events in some parts of Europe has increased as a consequence of increasing temperatures (Briffa et al., 2009; Hanel et al., 2018). It is expected that temperatures and the frequency and intensity of heat waves will continue to increase in the future (Kirtman et al., 2013; Vogel et al., 2017), directly affecting soil moisture and exacerbating the effects of a potential reduction in precipitation. In the future mean summer precipitation in the Mediterranean and Central Europe is predicted to decrease, and extreme events are expected to occur more frequently (Rajczak and Schär, 2017). Moisture in surface soil layers is predicted to decrease over the whole year in Southern Europe, and over summer and autumn in Central and Western Europe. Periods of very low soil moisture levels are expected to increase in frequency (Ruosteenoja et al., 2017). Feedback between soil moisture and air temperature additionally enhances temperature extremes (Vogel et al., 2017). Low soil humidity reduces evapotranspiration and increases heat flux, thus promoting the occurrence of higher air temperatures. On the other hand, higher air temperatures increase water vapour deficit, which contributes to the persistence of evapotranspiration despite decreasing soil moisture (Ruosteenoja et al., 2017). These changes will result in substantial negative effects on forest ecosystems and their biogeochemical cycling. The increasing frequency of extreme weather events will contribute to forest mortality and changes in forest communities due to greater sensitivity of tree seedlings to extreme weather events (tree seedlings experience the highest mortality rates) and increasing pressures on forests in marginal environments (Pickles and Simard, 2017). Apart from drought, forests under warmer and drier conditions will be prone to more frequent forest fires and insect attacks (Seidl et al., 2017). While there are a great deal of research data available on the effects of drought on the aboveground parts of common European tree species, tree roots and ectomycorrhizal fungi living in symbiosis with tree fine roots still remain relatively unexplored. Tree fine roots, which are usually defined as roots thinner than 2 mm in diameter, amount to less than 2 % of tree biomass in boreal and temperate forests. Nevertheless, they are an extremely active part of the forest ecosystem, as they absorb water and nutrients and contribute to carbon cycling because of their quick turnover rate (Brunner and Godbold, 2007).

Mycorrhizal fungi are among the key soil organisms for the functioning of forest ecosystems. In European temperate forests, the majority of stand forming tree species are ectomycorrhizal (Kraigher et al., 2013). In

ectomycorrhiza the fungal mantle ensheaths the tree fine root, and the hyphae penetrate between the cells of the root cortex and form a Hartig net. Via extramatrical mycelium comprised of hyphae and/or rhizomorphs (i.e. bundles of hyphae that may contain specialized structures for transport of water and solutes), ectomycorrhizal fungi grow in the surrounding substrate (Agerer, 2001) and create huge common mycelial networks connecting the tree root systems of neighbouring and even more distant trees (Simard and Durall, 2004; Simard et al., 2012). Common mycelial networks (CMN) connect trees of the same species or different tree and fungal species. CMN extend over tens of meters, and in some cases a single fungus can extend across hundreds of hectares of forest. In CMN large old trees, i.e. “mother trees”, act as hubs (Figure 1). CMN affect the establishment of tree seedlings and their survival, growth, physiology, health status and competitive ability. Via CMN, exchange of resources (carbon, water, nitrogen, phosphorus, micronutrients), stress molecules and allelochemicals occurs. Tree seedlings are colonized with ectomycorrhizal fungi via this pathway. Resource exchange follows the source-sink gradient. Stress signals can travel through CMN very quickly, in a time span of a few hours (Gorzela et al., 2015). Ectomycorrhizal hyphae or rhizomorphs grow to different extents into surrounding substrate, thus forming morphologically distinct exploration types of ectomycorrhizae (e.g. contact exploration type and short, medium and long distance exploration types), with some evidence of their different functional roles (Agerer, 2001). For example, the contact exploration type, which is characterized by a smooth mantle and only a few emanating hyphae, takes up substances mainly via the mantle, which is in close contact with the surrounding substrate, while the long distance exploration type exploits substrate which is several decimetres away through extensive rhizomorphs (Agerer, 2001).

Ectomycorrhizal fungi, with their morphological, physiological and ecological mechanisms, provide numerous benefits to forest ecosystems, such as colonization of larger soil volumes, colonization of tiny soil pores due to the smaller diameter of fungal hyphae compared to fine roots, increased nutrient absorption surface, release of poorly available macronutrients, secretion of exudates that improve availability of micronutrients, changes in soil pH in the mycorrhizosphere, redistribution of water and nutrients in time and space, and the establishment of connections between sources and sinks of carbon (Kraigher et al., 2013). To be able to predict the response of forest ecosystems to future environmental changes with greater accuracy, it is neces-

sary to understand the response of fine roots in connection with ectomycorrhizal fungi (Staddon et al., 2003).

2 EFFECTS OF DROUGHT ON TREE FINE ROOTS

To assure access to limited resources belowground, plants have developed different strategies for their belowground parts. These can be classified into five groups: architectural (e.g. ramification of root system, depth of rooting), morphological (e.g. root diameter, specific root length) and physiological (e.g. nutrient uptake kinetics, respiration, exudation) (Bardgett et al., 2014). Root trait variability among species and genotypes is huge, and above all, the root system is extremely plastic. The plasticity of the root system enables plants to adapt to variable environmental conditions, particularly with respect to water and nutrient access (Bardgett et al., 2014). Separate parts of the root system are located in soil layers or areas with different moisture levels, whereby water is passively distributed from moist to dry soil areas via tree roots. This process is called hydraulic distribution (Figure 2). When leaf stomata close and transpiration is minimal, plant water potential tends to equal soil water potential in areas where the most active roots are located, thereby wetting the dry soil in the surroundings. The most known type of hydraulic distribution is hydraulic lift, which occurs when deeper soil layers contain higher moisture levels than the surface soil (Prieto et al., 2012). Hydraulic lift can occur only in trees that form a deep root system, but also benefits neighbouring plants with shallower roots, e.g. combination of sessile oak (*Quercus petraea* (Matt.) Liebl.) and common beech (*Fagus sylvatica* L.) (Pretzsch et al., 2013), either directly via uptake of water that the tree with the deep root system releases into soil or indirectly via mycorrhizal fungi (Prieto et al., 2012).

In mixed stands competition among fine roots of different species can occur. In comparison to pure Norway spruce (*Picea abies* (L.) Karst) stands, the fine roots of Norway spruce in stands mixed with common beech are pushed towards the soil surface where they are potentially more prone to summer drought. In addition, spruce roots in mixed stands are less ramified and less colonized by long distance exploration types of ectomycorrhizal fungi. On the other hand, during spring drought, the presence of beech is beneficial for spruce, as there is less competition for water in mixed stands compared to pure spruce stands due to the deciduous nature of beech. Competition occurs only in spruce that are in the immediate vicinity of beech, which means that from the viewpoint of drought mitigation, spruce groups are more favourable compared to single spruce trees (Goisser et al., 2016).

Similar to the aboveground parts, tree roots respond to drought by using either avoidance or tolerance strategies. In drought avoidance water status between the belowground and aboveground parts is adjusted, balancing between water uptake and loss. In the short term, the tree avoids water loss by closing the leaf stomata, and in the longer term by reducing the growth of aboveground parts, leading to an increased root to shoot ratio. Water uptake can improve with the formation of a larger number of fine roots and deep roots seeking sources of water (Brunner et al., 2015).

Mechanisms of tolerance maintain continuous water transport, gas exchange and cell survival even at low water potentials, which is achieved through the adjustment of osmotic potential in roots with solute accumulation, increased resistance to cavitation through the strengthening of cell walls and reduction of xylem vessel diameter, and the ability of cells, particularly meristematic cells, to stay alive (Vilagrosa et al., 2012; Brunner et al., 2015). Roots, and fine roots in particular, are more prone to cavitation compared to the stem, both in broadleaves and conifers. Trees that grow in drier conditions are more resistant to cavitation compared to trees of the same species that grow under conditions of constant adequate moisture. Under extreme drought, cavitation of thinner roots protects the tree through hydraulic isolation from the surrounding drying soil. As long as leaf stomata remain closed, hydraulic isolation by cavitation in thinner roots prevents complete cavitation in the stem. When the drought is over, new root growth is established, hydraulic conductivity increases and cavitations fill up (Sperry and Ikeda, 1997). Drought reduces the occurrence of lenticels in woody fine roots, but its effect on the occurrence of growth rings in woody fine roots can vary between species of the same genus; in holm oak (*Quercus ilex* L.) drought reduced the occurrence of growth rings in woody fine roots, while in common oak (*Q. robur* L.) the occurrence of growth rings increased due to drought (Mrak et al., 2019).

In fine roots of common beech provenance seedlings, drought induced a decrease in carbon content, an increase in nitrogen content in some provenances and no change in nitrogen in others. Consequently, C to N ratio decreased in all provenances (Dounavi et al., 2016).

Fine root life span decreases in drought, except when there is hydraulic redistribution of moisture from areas with higher soil water content to areas with lower soil water content (McCormack and Guo, 2014). In addition, the biomass, length and root tip density of fine roots decreases in drought, while specific root length, root tissue density and root surface area index are not affected. However, these results are affected by how fine roots are

classified. When the diameter limit for fine roots was set at 0.5 mm instead of 2 mm, fine root biomass, specific root length and root tissue density increased due to drought, while fine root diameter and nitrogen content decreased (Brunner et al., 2015). In seedlings of common oak, the percentage of the finest roots (0.0–0.1 mm diameter) significantly increased, while the percentage of thicker fine roots decreased. In the same species, the mean diameter of fine roots decreased by 8.49 % (Mrak et al., 2019). In holm oak fine roots formed during the dry Mediterranean summer are thinner compared to those formed in other seasons (Montagnoli et al., 2019).

In drought conditions synthesis of suberin and lignin is increased. Suberin is located in the endodermis and exodermis of roots and in the periderm of roots that have undergone secondary growth. Suberinisation decreases water loss from the roots and improves water use efficiency. Cell wall lignification improves the mechanical resistance of cell walls and decreases water loss from the cells and dehydration. Due to increased levels of suberin and lignin in roots, the quantity and decomposition of soil organic matter changes, thereby affecting soil organic matter turnover. Only a limited number of organisms are capable of lignin degradation (brown rot fungi and actinobacteria). Drought may affect the (enzymatic) activity of these microorganisms. For lignin degradation in soil, the lignin to nitrogen ratio is crucial. Due to suberin, soil organic matter becomes more hydrophobic (Brunner et al., 2015).

3 EFFECTS OF DROUGHT ON SYMBIOSIS WITH ECTOMYCORRHIZAL FUNGI

Via extramatrical mycelium, water can be transferred from plants with access to the water supply in deeper soil layers to plants experiencing water shortage (Egerton-Warburton et al., 2007). This type of water supply is very important for the survival of tree seedlings (Lehto and Zwiazek, 2011). In drought prone forests, access to the CMN of mother trees is crucial for seedling establishment. Seedlings growing within the CMN of mother trees are larger and have better water use efficiency. The community of ectomycorrhizal fungi in seedlings is very similar to that in neighbouring adult trees. Connection to the CMN of adult trees must establish before the onset of the drought period; therefore, local drought adapted provenances with early germination and establishment of mycorrhizal connections are advantageous (Pickles and Simard, 2017). When severe droughts are expected, appropriate provenance selection and seedling life history are more important than the support of CMN. Seedlings of the same provenance established in tree nurseries are advantageous compared to

natural regeneration from seeds of the same provenance (Bingham and Simard, 2013). Mycelium with access to a water supply is able to survive in very dry soil (up to -2.5 MPa water potential or less). Hyphae are functionally active even after 68–77 days of drought and able to grow after 70–80 days of drought. Long distance water transport occurs via rhizomorphs in the symplast (Quejeta et al., 2003). Rhizomorphs are formed by fungi with hydrophobic cell walls, while water transport in hydrophilic fungi occurs via the apoplast. Knowledge on the relationship between the cell walls of mycorrhizal fungi and their resistance to drought is scarce (Lehto and Zwiazek, 2011). When exploration types of ectomycorrhizal fungi were compared in humid and drier *Pinus pinaster* Ait. stands, it was shown that long and short distance exploration types are significantly more abundant in drier conditions, while contact exploration types are more abundant in humid conditions. The abundance of medium distance exploration types was similar in both stands (Bakker et al., 2006). Pickles and Simard (2017) indicate that medium (*Amphinema*, *Boletus*, *Cortinarius*, *Tomentella*, *Tricholoma*) and long distance (*Rhizopogon*, *Suillus*) exploration types become dominant in seedlings under drought.

Findings on the effects of drought on ectomycorrhizal fungal colonization and structure of fungal communities vary widely, which can be ascribed to differences in experimental conditions (e.g. drought stress duration and intensity) and differences in selected ectomycorrhizal inoculi when inoculated seedlings were used. Globally, ectomycorrhizal colonization is lower in environments with large precipitation seasonality (Soudzilovskaia et al., 2015). In natural conditions, colonization by ectomycorrhizal fungi follows the moderate stress hypothesis, with greater colonization in conditions of moderate host plant stress and lower colonization in conditions of chronic stress. The lower colonization of ectomycorrhizal fungi in severe drought, when photosynthesis levels are low, helps to preserve the limited carbon supply, which would otherwise be spent to support fungi in exchange for nutrients, for plant survival (Swaty et al., 2004). In stands of *Quercus agrifolia* Née affected by multi-year drought, colonization with ectomycorrhizal fungi decreased (Quejeta et al., 2003). Comparison of *Pinus muricata* D. Don stands with 7 % and 13 % soil humidity showed that ectomycorrhizal colonization was greater in conditions of 13 % soil humidity (Kennedy and Peay, 2007). On the other hand, moderate drought did not affect colonization in beech seedlings (*Fagus sylvatica* L.) with natural present mycorrhiza (Shi et al., 2002) and beech seedlings inoculated with five species of ectomycorrhizal fungi (Pena and

Polle, 2014). In addition, ectomycorrhizal colonization rate did not change in a drought experiment with oak seedlings, and there was no significant effect on species richness (Mrak et al., 2019). However, species richness can be affected by plant genotype. Species richness in a drought resistant genotype of *Pinus edulis* Engelm. was two times higher than that in a drought sensitive genotype. When both genotypes were exposed to drought conditions, the structure of the ectomycorrhizal fungal community in the drought sensitive genotype changed, while no changes were recorded in the drought resistant genotype (Patterson et al., 2019).

Drought often results in changes in the abundance of certain ectomycorrhizal fungi (Shi et al., 2002; Swaty et al., 2004; Herzog et al., 2013; Pena and Polle, 2014; Mrak et al., 2019), e.g. the abundance of ectomycorrhizal fungi from the *Tomentella* genus decreased in a drought sensitive pine genotype (Patterson et al., 2019). A similar response was detected in oak seedlings exposed to drought, while the abundance of *Sphaerospora brunnea* (Alb. & Schwein.) Svrcek & Kubicka and *Thelephora* sp. increased (Mrak et al., 2019). Changes in fungal community structure towards drought resistant ectomycorrhizal fungi (or fungi that can cope with very limited carbon supply) would be beneficial for the host plant, as the fungi would potentially still provide several services to the plant. In stress conditions the uptake of macronutrients (N and P) into the plant is disturbed, and ectomycorrhizal fungi could reduce this deficiency to a certain extent.

In laboratory conditions it was found that ectomycorrhizal species *Cenococcum geophilum* Fr. (Figure 3) response to drought stress is lower compared to other ectomycorrhizal fungi (Jany et al., 2003; di Pietro et al., 2007). This species sustains the functionality of ectomycorrhizal fine roots, enabling immediate response to available water after the end of the drought period (Jany et al., 2003). Increased colonization rate of *C. geophilum* is common in stress conditions, including drought (Bakker et al., 2006; Grebenc & Kraigher, 2007, Kraigher in sod. 2007, Kraigher in sod. 2011). Under drought, the regulation of two types of aquaporins in this fungal species changes, but no significant positive correlation between physiological parameters of trees and mycorrhization with *C. geophilum* was discovered (Peter et al., 2016). The abundance of this species is also greater under elevated air temperatures and correlates positively with the growth of the aboveground part (Herzog et al., 2013). As the hyphae of *C. geophilum* are melanized, they are very resistant to decomposition after death. Accumulation of melanized remnants in the soil contributes to increased soil organic matter (SOM). Decomposition of melanized remnants is strongly in-

fluenced by the melanin to N ratio, similar to the lignin to N ratio in fine roots (Fernandez and Koide, 2014).

The enzymatic activity of ectomycorrhiza, which is related to the release of C, N and P from complex organic matter in the soil, is higher compared to non-mycorrhizal roots and remains elevated despite limited water access. It is dependent on the species of ectomycorrhizal fungus and decreases in the following order: *Suillus granulatus* (L.) Roussel > *Rhizopogon roseolus* (Corda) Th. Fr. > *Paxillus involutus* (Batsch) Fr. > *C. geophilum* (Kipfer et al., 2012). Nitrogen supply in the form of NH_4^+ from *C. geophilum* during drought is very low compared to other ectomycorrhizal fungi. The capacity for N uptake from dry soil is also related to other environmental parameters, e.g. sun exposure (Pena and Polle, 2014). In *C. geophilum* enzymatic activity increases only in drought combined with high temperatures and depends on host plant species (Herzog et al., 2013).

From the point of view of the plant, the presence of ectomycorrhizal fungi in drought conditions has many positive effects. It improves plant water potential, preserves hydraulic conductivity, increases the rate of photosynthesis compared to non-mycorrhizal seedlings, diminishes the negative effects of drought to aboveground and belowground parts, reduces effects on the structure of wood, delays the death of root tips, mitigates the reduction in leaf P content and reduces oxidative stress (Ortega et al., 2004; Walker et al., 2004; Alvarez et al., 2009a; Alvarez et al., 2009b; Beniwal et al., 2010; Kipfer et al., 2010; Danielsen and Polle, 2014). In drought conditions ectomycorrhizal root tips may increase their osmotic potential with accumulation of soluble sugars and sugar alcohols or polyols (fungal products) to sustain the uptake of water (Shi et al., 2002).

4 CONCLUSIONS

The root system of trees is very plastic, enabling a multitude of adaptations to drought conditions. Adaptations occur in the growth and development of tree roots, morphology, anatomical and biochemical properties and biological interactions (Figure 2). Although the main mechanisms of adaptations are known, there are still many unknowns in this field of study, particularly with respect to biotic and abiotic interactions, which make it impossible to immediately transfer theoretical knowledge into forest planning. Climate change towards warmer and drier conditions will most affect tree seedlings due to their underdeveloped root system. Although adult trees may support seedlings via common mycelial networks, in cases where severe droughts are expected, proper selection of tree seedling provenances will be of great importance.