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Mnogotere vloge silicija izboljšajo uspevanje rastlin

Multiple roles of silicon benefit plants

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Izvleček: Prispevek na podlagi širokega pregleda literature obravnava vlogo silicija pri rastlinah, od same pojavnosti silicija v tleh preko mehanizmov privzema in prenosa, do nalaganja in deleža silicija v rastlinah. Članek nadalje zajema evolucijski vidik pojavnosti silicija pri rastlinah ter izpostavlja njegove ključne vloge pri uspevanju rastlin in blaženju negativnih učinkov številnih stresnih dejavnikov ter njegovo uporabnost v kmetijstvu.

Ključne besede: silicij, rastline, evolucija, blaženje stresa, kmetijstvo

Abstract: This paper includes broad literature review about silicon in plants from its appearance in soils to mechanisms of uptake and transport, and finally accumulation and content of silicon in plants. Furthermore, the evolutionary aspect of silicon in plants and its key role for plant growth and development by mitigating negative effects of various stress factors is highlighted along with its application in agronomy.

Keywords: silicon, plants, evolution, stress mitigation, agronomy

Uvod

Silicij (Si) zaseda drugo mesto med najpogostejšimi elementi, ki se pojavljajo v tleh (Epstein 1994) in v zemeljski skorji, takoj za kisikom (O) (Mason 1966). Glede na njegovo vsesplošno prisotnost lahko torej sklepamo, da ga preko korenin v svoja tkiva privzemajo tudi rastline (Ma in Takahashi 2002).

Prva navedba o vsebnosti Si v rastlinah sega že v začetek 19. stoletja (de Saussure 1804). Si v rastlinah najdemo v zelo različnih, a pomembnih deležih njihove suhe mase. Te vrednosti običajno segajo vse od 0,1 do 10 % ali celo več (Epstein 1994, Epstein in Bloom 2005, Hodson in sod. 2005). Ob primerjavi z esencialnimi makrohranili (dušik (N): 0,5–6 %, fosfor (P): 0,15–0,5 %, kalij (K): 0,8–8 %, žveplo (S): 0,1–1,5 %, kalcij (Ca): 0,1–6 % in magnezij (Mg): 0,05–1 %) (Epstein 1983, 1994, Epstein in Bloom 2005) ugotovimo, da največjo variabilnost glede pojavljanja v rastlinah kaže ravno Si. Vendar pa so tudi njegove najnižje izmerjene vrednosti v rastlinah popolnoma primerljive z nizkimi vrednostmi nekaterih makrohranil (Epstein 1994, 1995, 1999). Si je torej tako pomemben gradnik tal kot tudi rastlin (Epstein 1994).

Kljub njegovi veliki zastopanosti v rastlinskem svetu, predvsem pri travah (Epstein 1999), Si ne prištevamo med esencialne elemente (Jones in Handreck 1967), z izjemo presličevk (Equisetaceae) (Chen in Lewin 1969) ter kremenastih (Bacillariophyceae) in zlatorjavih alg (Chrysophyceae) (Darley in Volcani 1969, Lewin in Reimann

1969, Kaufman in sod. 1981). Iz tega razloga ga pri pripravi običajnih hranilnih raztopin za gojenje rastlin pogosto izpuščajo, vendar pa so na tak način vzgojene rastline neke vrste eksperimentalni artefakti (Huang in sod. 1992, Epstein 1994, 1995, 2009, Shakoor 2014). Obstaja namreč vrsta raziskav, ki so pokazale pojav simptomov pomanjkanja pri rastlinah, gojenih v hranilnih raztopinah brez Si (Miyake in Takahashi 1978, 1983a, 1985, 1986). Epstein (1994, 1999) trdi, da je nepriznavanje Si kot esencialnega elementa po eni strani posledica težavne popolne odstranitve Si iz gojitvenega medija in s tem nezmožnosti priprave prave kontrole brez Si. Prav iz tega vzroka Woolley (1957) ni opazil razlik med rastlinami, gojenimi ob dodatku Si, ter rastlinami, gojenimi v odsotnosti Si. Glavni razlog za nepriznavanje esencialnosti Si pri rastlinah pa se po mnenju Epsteina (1994, 1999) skriva v vsesplošno sprejeti klasični definiciji esencialnosti, ki sta jo postavila Arnon in Stout (1939). Šele v zadnjem času se je definicija esencialnosti nekoliko spremenila in tako kot esencialne lahko obravnavamo elemente, ki izpolnjujejo vsaj enega od sledečih dveh kriterijev: (1) elemente, ki so del molekul, bistvenih za strukturo ali metabolizem rastline ter (2) elemente, katerih pomanjkanje povzroči odstopanja v rasti, razvoju ali razmnoževanju rastlin v primerjavi z rastlinami, ki takšnega pomanjkanja nimajo (Epstein in Bloom 2005). Glede na posodobljeno definicijo esencialnosti elementov bi morala esencialnost Si slej ko prej postati splošno priznana znotraj celotnega kraljestva rastlin (Liang in sod. 2007). Prvi pomembnejši korak na tej poti predstavlja letno srečanje združenj ASA (American Society of Agronomy), CSSA (Crop Science Society of America) in SSSA (Soil Science Society of America) leta 2012, na katerem je organizacija AAPFCO (Association of American Plant Food Control Officials) Si uradno imenovala kot koristen element za rastline na podlagi njegovih številnih že prepoznanih pozitivnih učinkov tako na Si-akumulirajoče kot neakumulirajoče vrste (USDA ARS 2012, Heckman 2013).

Za razliko od številnih drugih elementov, ki v tleh niso tako pogosti kot Si in katerih kopičenje v rastlinah je posledično v veliki meri odvisno od razmer v okolju, je količina Si v rastlinah odvisna predvsem od njihovega načina privzema Si, ki se razlikuje med vrstami (Ma in Takahashi 2002, Cooke in Leishman 2011a). Že Jones in Handreck (1967) sta na osnovi suhe mase kulturnih rastlin predlagala ločevanje treh skupin glede na količino Si v njihovih tkivih. To so: (1) dvokaličnice s koncentracijami Si okrog 0,1 %, (2) trave sušnih območij, kot sta oves in rž z okrog 1 % Si, ter (3) trave mokrotnih območij, npr. riž, z najvišjimi koncentracijami Si – okrog 5 % in celo več. V kasnejših letih so tovrstno delitev iz zgolj kulturnih razširili tudi na nekulturne rastline (Ma in Takahashi 2002). Ma in Takahashi (2002) sta ugotovila, da s Si bogate vrste običajno hkrati odražajo tudi nizke koncentracije Ca, in obratno. Opredelila sta tri načine privzema in posledično tri tipe rastlin glede na njihovo vsebnost Si in Ca: (1) akumulatorje Si, pri katerih koncentracija Si običajno presega 1 % in imajo razmerje Si/Ca > 1, (2) izključevalce Si s koncentracijo Si pod 0,5 % in razmerjem Si/Ca < 0,5 ter (3) intermediate z zmernimi koncentracijami Si, ki jih ne moremo uvrstiti v nobenega od obeh prej navedenih tipov (Preglednica 1).

Preglednica 1: Kriteriji za opredelitev tipa rastlin glede na stopnjo akumulacije silicija (Si). Podan je tudi način privzema Si pri obravnavanih tipih. Prirejeno po Ma in Takahashi (2002).
Table 1: Criteria for determining plant type according to silicon (Si) accumulation rate, with type of Si uptake also defined for each plant type. Adapted from Ma and Takahashi (2002).

	Tip rastline		
	Akumulatorji Si	**Intermediati**	**Izključevalci Si**
Vsebnost Si (%)	> 1	1–0,5	< 0,5
Razmerje Si/Ca	> 1	1–0,5	< 0,5
Stopnja akumulacije Si	+	±	-
Način privzema Si	aktiven	pasiven	preprečevanje privzema

Visoke koncentracije Si zaznamo tako med evolucijsko primitivnejšimi mahovi in določenimi praprotnicami (lisičjačnice, presličnice in nekatere praproti) kot tudi med evolucijsko naprednejšimi enokaličnicami (ostričevke in trave). Pri travah Si običajno predstavlja do 4 % njihove suhe mase, pri preslicah do 16 %, medtem ko pri rižu vrednosti lahko segajo vse do 20 % (Lewin in Reimann 1969). Med intermediate sodijo bučevke, koprivovke, murvovke in komelinovke, ostale skupine pa kopičijo manj Si (Ma in Takahashi 2002).

Razlike v količini Si niso opazne le med vrstami, temveč celo med različnimi genotipi znotraj vrst (Deren in sod. 1992, Ma in sod. 2003). Ta pojav bi lahko razložili na podlagi razlik v sposobnosti korenin za privzem Si ter razlik v zmožnosti kopičenja in načina prerazporejanja Si (Ma in Takahashi 2002, Ma in sod. 2003).

Najnovejše raziskave kažejo, da potencial rastlinskih vrst za kopičenje Si lahko zelo zanesljivo ocenimo na podlagi molekularnih analiz Lsi1 prenašalcev Si. Določene značilnosti teh prenašalcev so namreč zelo ohranjene pri vseh vrstah, kjer se pojavljajo. Posledično lahko na podlagi njihove prisotnosti oz. odsotnosti ocenimo potencial različnih rastlinskih vrst za kopičenje Si in tako obstoječi umestitvi vrst med akumulatorje Si, intermediate ali izključevalce Si dodamo molekularno podporo. Poleg tega na podlagi navedenih analiz lahko ocenimo tudi, katerim rastlinskim vrstam bi dodajanje Si najbolj koristilo (Deshmukh in sod. 2015, Cooke in sod. 2016a, Deshmukh in Bélanger 2016).

Privzem, prenos in nalaganje silicija v rastlinah

Privzem in prenos silicija po rastlinah

V tleh se Si večinoma pojavlja v obliki Si kisline (H_4SiO_4), ki je rezultat kemijske erozije silikatnih mineralov (Basile-Doelsch in sod. 2005), in sicer v koncentracijah med 0,1 in 0,6 mM (Epstein 1994). Te so popolnoma primerljive s koncentracijami mnogih za rastline pomembnih anorganskih hranil, kot sta npr. K in Ca, ter celo močno presegajo koncentracije, značilne za fosfat (Epstein in Bloom 2005).

Rastline Si privzemajo preko korenin v obliki nenabite in hidrirane Si kisline (Raven 1983). Privzem poteka vsaj v dveh fazah: najprej nastopi radialni prenos Si iz zunanje raztopine v celice skorje korenin, temu pa sledi faza nalaganja Si iz skorje v ksilem (Mitani in Ma 2005). Casey in sod. (2003) so v ksilemskem soku pšenice Si zaznali le v obliki mono- ter disilicijeve kisline, in sicer v razmerju 7:1. Prenos Si po rastlini poteka po apoplastni poti preko ksilema (Raven 1983) v nepolimerizirani obliki (Epstein 1994). Mehanizmi, ki preprečujejo polimerizacijo Si med prenosom po ksilemu, bi bili lahko vezani na interakcije med Si in organskimi spojinami (Kaufman in sod. 1981). Prenos Si po rastlini poganja transpiracijski tok (Yoshida in sod. 1962a, Ma in Takahashi 2002), a vseeno je pri tem vpletena tudi aktivna komponenta (Liang in sod. 2006a).

Kot nakazano že v prvem poglavju, obstaja več načinov privzema Si. Poznani so trije mehanizmi. Za nekatere vrste, npr. riž, je značilen energetsko odvisen aktiven način privzema s prenašalci v celičnih membranah (Tamai in Ma 2003, Mitani in Ma 2005), za druge kot npr. oves ali kumara s transpiracijo pogojen pasiven način privzema (Jones in Handreck 1965, Faisal in sod. 2012), preostale vrste (npr. paradižnik) pa privzem Si preprečujejo (Ma in Takahashi 2002). Parry in Winslow (1977) sta kot možen razlog za nizke koncentracije ter preprečevanje privzema Si pri nekaterih vrstah navedla impregnacijo koreninskih laskov s tanko plastjo kutinu ali suberinu podobne maščobne snovi, ki ovira privzem Si. Nikolic in sod. (2007) pa so ugotovili, da je tudi preprečevanje privzema Si metabolno aktiven proces. Liang in sod. (2005a) so v svoji raziskavi prišli do zaključka, da način privzema Si v rastline ni nujno striktno določen za vsako vrsto posebej, temveč je pri nekaterih vrstah možen preklop med aktivnim in pasivnim načinom glede na razpoložljivost Si v tleh. Tako so pri kumari, za katero v splošnem velja pasiven način privzema, ugotovili, da v primeru nizkih koncentracij Si pobudo prevzame aktivna komponenta privzema (Liang in sod. 2005a). Do podobnih ugotovitev so prišli tudi pri nekaterih drugih vrstah (Van der Vorm 1980, Henriet in sod. 2006, Liang in sod. 2006a). Z aktivnim načinom privzem Si poteka hitreje kot privzem vode, zato je vsebnost Si v rastlini višja kot v zunanji raztopini. Za pasiven privzem je značilno, da je koncentracija

Si v rastlini in v zunanji raztopini zaradi podobne hitrosti privzema Si in vode podobna, v primeru preprečevanja privzema Si pa je privzem Si v rastlino počasnejši od privzema vode ter skladno s tem koncentracija Si v rastlini nižja v primerjavi z zunanjo raztopino (Ma in sod. 2001b, Mitani in Ma 2005, Cooke in Leishman 2011a). Način privzema Si ter skladno s tem tudi njegova količina v rastlinah sta odvisna od stopnje transpiracije ter ravnovesja med potrebo rastlin po Si ter razpoložljivostjo Si v tleh (Faisal in sod. 2012). Dietrich in sod. (2003) so pokazali, da je pri travah količina nakopičenega Si v rastlinah znotraj iste vrste lahko zelo različna glede na razpoložljivost Si v tleh. Koncentracija rastlinam dostopnega Si je v prvi vrsti odvisna od samega procesa kroženja Si med tlemi in rastlinami (Haynes 2014), nanjo pa vplivajo tudi pH tal, delež gline, mineralov in organske snovi ter železovih (Fe) oz. aluminijevih (Al) oksidov oz. hidroksidov, kar se navezuje na geološko starost tal. Geološko mlajša tla vsebujejo višje koncentracije rastlinam dostopnega Si kot močno erodirana tla (Tubana in sod. 2016). Topnost rastlinam dostopnega Si v tleh se povečuje z višanjem pH tal (Haynes 2014).

Ma in sod. (2001a) so v raziskavah z rižem ugotovili, da največjo vlogo pri privzemu Si igrajo stranske korenine in ne koreninski laski. Za riž je namreč značilen energetsko odvisen aktiven način privzema Si preko specifičnih prenašalcev za privzem Si kisline, ki jih v koreninskih laskih najverjetneje ni (Ma in sod. 2001a). Aktiven način privzema omogoča rižu kopičenje daleč največjih količin Si med vsemi vrstami (Ma in sod. 2002, 2004b). Razlog za nižjo vsebnost Si pri vrstah s pasivnim privzemom je nižja gostota prenašalcev (Mitani in Ma 2005).

Do sedaj so odkrili že več genov, ki kodirajo prenašalce Si. Raziskovanje na temo prenašalcev Si se je pričelo z rižem, ki je skladno s tem tudi najbolj raziskana vrsta na področju prenašalcev Si (Ma in sod. 2006, 2007, Yamaji in Ma 2007, Yamaji in sod. 2008, Yamaji in Ma 2009, Sakurai in sod. 2015). Nekaj raziskav na to temo obstaja tudi pri koruzi in ječmenu (Chiba in sod. 2009, Mitani in sod. 2009a,b, Yamaji in sod. 2012), v posameznih raziskavah pa so se s prenašalci Si ukvarjali tudi pri muškatni buči, kumari, pšenici in soji (Mitani-Ueno in sod. 2011, Mitani in sod. 2011, Montpetit in sod. 2012, Deshmukh in sod. 2013, Wang in sod. 2015).

Nalaganje silicija v rastlinah

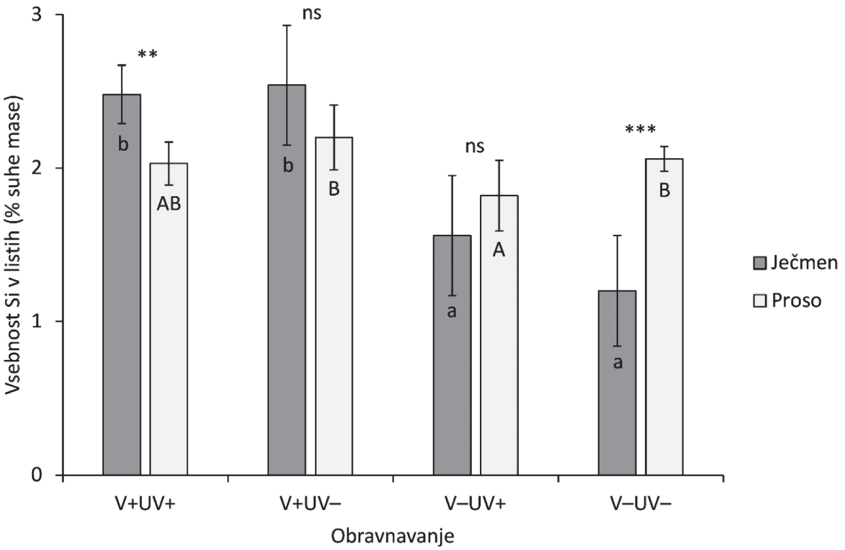
Do nasičenja Si kisline znotraj rastline pride pri koncentraciji 1,67 mM, čemur sledita polimerizacija in odlaganje (Cooke in Leishman 2011a). Si se nalaga predvsem v celičnih stenah, a tudi v medceličnih prostorih, lumnu celic ter zunanjih plasteh v trdni amorfni hidrirani obliki silicijevega dioksida (SiO_2 x nH_2O) (Marschner in sod. 1990, Epstein 1994). V začetnih fazah odlaganja in posledično pri nižjih koncentracijah se Si pojavlja v t.i. silicijevih celicah, sčasoma ter z naraščajočo koncentracijo pa nastaja vedno več silicijevih telesc ali fitolitov (Ma 1990). Tako imenujemo vrastke celične stene v celico, ki se bolj ali manj v celoti zapolnijo s Si (Sangster in Parry 1981). Poleg silicijevega dioksida in vode manjši delež mase fitolitov (običajno do 5 %) prispevajo tudi nekateri drugi elementi, kot so Al, Fe, mangan (Mn), Mg, P, baker (Cu), N in ogljik (C) (Beavers in Jones 1963, Jones in Milne 1963, Wilding in sod. 1967). Njihovi deleži se razlikujejo med različnimi kultivarji (Li in sod. 2014). Si se lahko pojavlja tudi samostojno ali v kombinaciji s kalcijevim karbonatom v izrastkih celičnih sten, imenovanih cistoliti (Piperno 2006). Stopnja tvorbe fitolitov v rastlinah je odvisna od številnih dejavnikov, npr. podnebja v njihovem okolju, tal in vsebnosti vode v tleh, starosti rastlin, najpomembnejši vpliv pa ima nagnjenost same vrste k tvorbi fitolitov. Vse vrste namreč ne tvorijo fitolitov. Fitoliti se v rastlinskem svetu pojavljajo v zelo različnih vrstno značilnih oblikah in velikostih (Piperno 2006), ki običajno segajo med 2 in 60 μm (Meunier in sod. 1999). Z namenom preprečevanja zmede zaradi pojavljanja različnih poimenovanj enakih oblik fitolitov so Madella in sod. (2005) postavili uradno nomenklaturo za standardizacijo poimenovanj vseh različnih oblik fitolitov. Golokhvast in sod. (2014) so našli povezavo med različnimi morfotipi fitolitov in evolucijsko starostjo rastlin. Fitoliti evolucijsko starejših taksonov so v splošnem večji kot pri evolucijsko mlajših taksonih. Poleg tega se pri evolucijsko starejših skupinah pojavlja manj različnih morfotipov fitolitov kot pri mlajših (Golokhvast in sod. 2014). Velikost fitolitov znotraj rodu naj bi korelirala tudi s stopnjo ploidnosti, kar so ugotovili pri poliploidnih pšenicah (Hodson 2016). Poleg vrstno značilnih oblik in s tem možnosti uporabe na področju taksonomije (Rovner

1971, Lu in sod. 2009, Lisztes-Szabó in sod. 2014, Out in Madella 2016) ter anorganskega značaja in posledično večje odpornosti na razpadanje fitolite odlikuje tudi izjemna obstojnost (Piperno 2006). Strömberg (2004) je uspešno izolirala 35 milijonov let stare fitolite, Jones (1964) pa je poročal celo o prisotnosti fitolitov v 60 milijonov let starih sedimentih. Fitoliti tako predstavljajo uporabno in zanesljivo orodje za arheološke in paleoekološke raziskave vse do začetka kenozoika (Rovner 1971, Piperno 2006).

Silicij se najpogosteje kopiči v povrhnjici ali njeni bližini (Yoshida in sod. 1962a, Prychid in sod. 2004), npr. v buliformnih celicah listov trav (Sangster in Parry 1969), v tvorbah povrhnjice kot so trihomi (Kaufman in sod. 1981) in listne reže (Lu in sod. 2009), v celicah žilne ovojnice (Prychid in sod. 2004) ter tudi v mezofilu (Morikawa in Saigusa 2004). Silicijeve celice se pogosteje pojavljajo v žilah, silicijeva telesca pa se običajno nanašajo na buliformne celice (Ma 1990). Pri travah pogosto govorimo o dvojni plasti, ki jo tik nad povrhnjico tvorita odložen Si in kutikula (Yoshida in sod. 1962b, Currie in Perry 2007). Ko se Si odloži v tarčnih celicah, njegovo prerazporejanje ni več mogoče (Raven 1983, Epstein 1994). Motomura in sod. (2004) so sprva trdili, da sta možna tako pasiven kot aktiven način odlaganja Si, odvisno od tipa celic. Kasnejše raziskave so pokazale, da je odlaganje Si izključno aktiven proces, ki vključuje pozitivno kontrolo (Motomura in sod. 2006, Markovich in sod. 2015). Idioblasti, katerih notranjost je popolnoma zapolnjena s Si, so odmrle celice v procesu programirane celične smrti (Markovich in sod. 2015, Kumar in Elbaum 2018). Vzrok za njihovo smrt kljub temu ne tiči v nalaganju Si, temveč gre zgolj za eno od faz njihovega razvoja (Markovich in sod. 2015). Pri teh celicah na določeni razvojni stopnji pride do zelo nagle izgube jedra ter citoplazme in s tem priprave prostora za odlaganje Si struktur (Blackman 1969). V zgodnji fazi njihovega razvoja lahko opazimo zelo obsežno jedro ter veliko število mitohondrijev, kar nakazuje že vnaprej določeno nagnjenost teh celic k visoki stopnji aktivnosti (Sangster in sod. 2001). Law in Exley (2011) sta ugotovila, da je obarjanje in s tem nalaganje Si v rastlinah oz. biosilicifikacija tesno povezana s polisaharidom kalozo, ki sproži proces biosilicifikacije. Pred silicifikacijo nastopi še proces lignifikacije (Zhang in sod. 2013a). Piperno in sod. (2002) ter Dorweiler in Doebley (1997) so našli neposredno povezavo med ligninom in fitoliti na genetski ravni, saj so ugotovili, da nastanek fitolitov nadzorujejo isti geni kot nalaganje lignina. Si se lahko nalaga tako v koreninah (Parry in Kelso 1975, Sangster 1977, 1978a,b, Bennett 1982, Parry in sod. 1984, Hodson in Sangster 1989a,b), listih (Parry in Smithson 1964, Sangster 1968, Sangster in Parry 1969, Sangster 1970, Hayward in Parry 1975, Parry 1975, Hodson in Sangster 1988a, Lanning in Eleuterius 1989, Larcher in sod. 1991), kot tudi ovršnih listih socvetij (Parry in Smithson 1966, Soni in Parry 1973, Parry in Hodson 1982, Hodson in Bell 1986, Hodson in Sangster 1988b, 1989c). Zaznali so ga celo v iglicah iglavcev (Hodson in Sangster 1998, 2002). V obliki fitolitov ga v splošnem lahko najdemo v vseh rastlinskih delih, še najmanj pogosto v koreninah (Prychid in sod. 2004). Tudi Lux in sod. (1999) so v koreninah zaznali znatno manj Si kot v listih. Pri mladih koreninah se Si nabira izključno v endodermalni plasti, pri starejših rastlinah pa ga najdemo tudi v povrhnjici, skorji in prevajalnih tkivih korenin (Sangster 1978b).

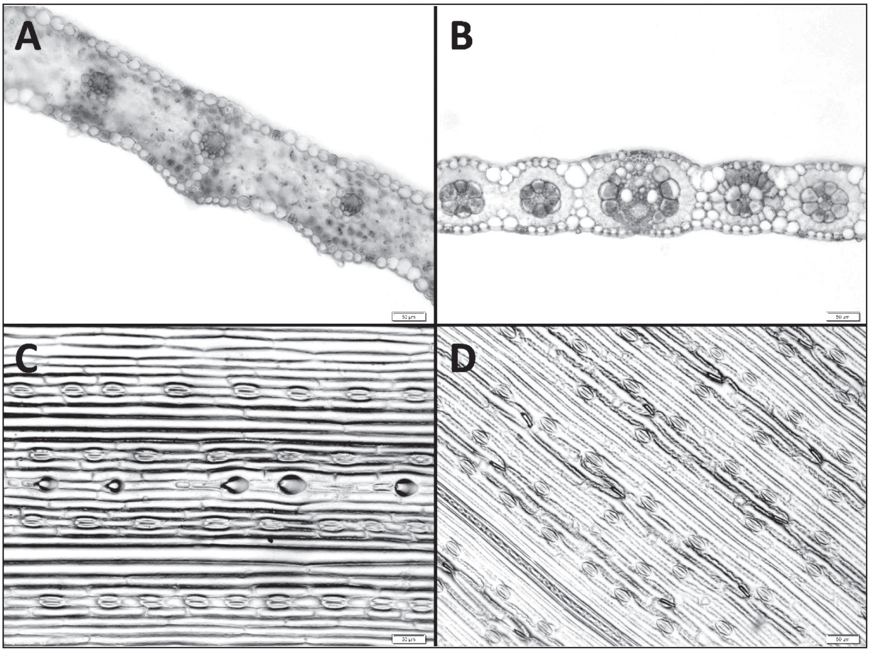
Pri koreninah so zaznali filogenetsko pogojene razlike v vzorcu nalaganja Si (Sangster 1978b, Parry in sod. 1984). Razlike v vzorcu nalaganja Si pri rastlinah so zaznavne tako na ravni družin (Currie in Perry 2007) kot tudi med posameznimi vrstami, znotraj vrst (Hartley in sod. 2015) ter celo med različnimi funkcionalnimi tipi rastlin, npr. med C_3 in C_4 vrstami (Kaufman in sod. 1985, Lanning in Eleuterius 1989). V primeru vrst sta ključna dejavnika, ki lahko privedeta do omenjenih razlik, povzročena škoda na rastlinah s strani rastlinojedov ali izboljšana preskrba rastlin s Si (Hartley in sod. 2015). Poleg tega na privzem in nalaganje Si zagotovo vplivajo tudi razni abiotski dejavniki, ki lahko prikrijejo vpliv rastlinojedov (Herranz Jusdado 2011). Vzorec nalaganja Si se lahko razlikuje glede na razvojno fazo rastlin. Hodson in Sangster (1988a) sta tako opazila, da se Si v primeru mladih listov pšenice nabira predvsem v celicah spodnje, v primeru starejših pa tudi v celicah zgornje povrhnjice. V ovršnih listih se največ Si nabira v zunanjih stenah celic povrhnjice (Hodson in Sangster 1989c). Poleg tega se tekom razvoja rastlin zaradi spreminjajočih se razmerij med vgrajenimi polisaharidi v novo nastajajočih celičnih stenah razlike kažejo tudi v smislu oblike nalaganja Si znotraj celic (Perry in sod. 1987).

Primerjava vsebnosti Si v listih C_3 vrste, ječmena (Grašič in sod. 2019a), in C_4 vrste, prosa (Grašič in sod. 2019b), pri štirih različnih obravnavanjih (kombinacije zadostne dostopnosti vode in pomanjkanja vode ter naravne ravni UV sevanja in zmanjšane ravni naravnega UV sevanja) pri podobnih okoljskih razmerah je pokazala, da sta pomanjkanje vode in pomanjkanje naravnega UV sevanja na privzem Si bolj omejujoče vplivala pri ječmenu (Grašič in sod. 2019a,b). Razlike v vsebnosti Si v listih pri različnih obravnavanjih so bile pri prosu majhne, zato je do razlike v vsebnosti Si v listih med obema proučevanima vrstama prišlo le pri obeh ekstremnih obravnavanjih (Slika 1). Slika 2 prikazuje morfološko primerjavo lista ječmena in prosa.



Slika 1: Vsebnost silicija (Si) v listih ječmena in prosa pri štirih obravnavanjih z različno dostopnostjo vode (V) in naravnega UV sevanja (UV). Prikazane vrednosti so povprečja ± standardna deviacija; n = 5 (ječmen) ali 6 (proso) za vsako obravnavanje. Statistično značilne razlike med obravnavanji pri ječmenu so označene z malimi tiskanimi črkami, pri prosu pa z velikimi tiskanimi črkami ($p \leq 0{,}05$; Duncanovi testi). Zvezdice prikazujejo statistično značilne razlike med ječmenom in prosom znotraj istega obravnavanja (*, $p \leq 0{,}05$; **, $p \leq 0{,}01$; ***, $p \leq 0{,}001$; ns, ni značilnih razlik; Studentov t-test) (Grašič in sod. 2019a,b).

Figure 1: Silicon (Si) content for barley and proso millet leaves, grown under four treatments with different water availability (V) and natural UV radiation (UV). Data are means ± SD; n = 5 (barley) or 6 (millet) for each treatment. Significant differences between the four treatments are indicated with lower case letters for barley and with upper case letters for proso millet ($p \leq 0.05$; Duncan tests). Asterisks demonstrate significant differences between barley and proso millet within each treatment (*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$; ns, not significant; Student's t-test) (Grašič et al. 2019a,b).



Slika 2: Prečni prerez lista ječmena (A) in prosa (B) ter odtis povrhnjice lista ječmena (C) in prosa (D) z vidnimi listnimi režami, bodičkami in fitoliti. Povečava, 100x; dolžina merila, 50 µm.

Figure 2: Cross-section of a barley (A) and proso millet leaf (B), and epidermal impression of a barley (C) and proso millet leaf (D) with visible stomata, prickle hairs and phytoliths. Magnification, 100x; scale bar length, 50 µm.

Evolucijski vidik silicija pri rastlinah

Silicij za rastline z energetskega vidika predstavlja 10–20 krat manj potraten vir od C in tako predstavlja alternativo C predvsem s strukturnega in podpornega vidika, s tem pa pripomore k boljšemu ravnovesju C v rastlinah (Raven 1983, McNaughton in sod. 1985, O'Reagain in Mentis 1989, Cooke in Leishman 2011b). Schoelynck in sod. (2010) so pri travah iz mokrotnih travnikov zaznali negativno korelacijo med koncentracijo biogenega Si ter koncentracijo z energetskega vidika zahtevnejšega lignina. Rastlinam z več vgrajenega Si so pripisali tekmovalno prednost zaradi večje možnosti vlaganja energije tudi v druge procese (Schoelynck in sod. 2010). Podobno sta razmišljali tudi Cooke in Leishman (2011b) na podlagi ugotovitve, da listi s krajšo življenjsko dobo vsebujejo večje količine Si v primerjavi z bolj dolgoživimi listi. Sklepali sta, da se jim zaradi kratkoživosti vgrajevanje Si kot metabolno cenejše surovine izplača bolj kot vključevanje C v svoja tkiva (Cooke in Leishman 2011b).

V splošnem je o številnih koristih Si za rastline znanega že veliko, kar bo natančneje opisano v sledečih poglavjih. S tem se poraja vprašanje, zakaj se Si ne pojavlja v večjih količinah pri vseh rastlinskih vrstah (Raven 1983, Piperno 2006). Za odgovor na to vprašanje je potrebno ovrednotiti tudi ceno vgrajevanja Si namesto C, o čemer pa za zdaj vemo dokaj malo (Cooke in Leishman 2011a). Cena, ki jo morajo rastline plačati ob vgrajevanju Si namesto C, je najverjetneje povezana s povečanjem gostote in s tem večjim stroškom za izgradnjo mase (Raven 1983) ter z zmanjšano prožnostjo. Dodatno slabost Si v primerjavi s C bi lahko predstavljala omejitev glede prerazporejanja Si struktur po njihovem odlaganju v rastlinah ter glede sposobnosti tvorbe različnih kompleksnejših spojin. Exley (1998) je namreč v svoji raziskavi ugotovil, da v naravi povezave Si-O-C ter Si-C ne obstajajo. V nasprotju s tem sta Weiss in Herzog

(1978) poročala o prisotnosti organskih Si kompleksov pri vrsti *Thuja plicata* Donn ex D.Don. Še ena možna omejevalna okoliščina v povezavi s Si je razvidna v stresnih razmerah, ko je za učinkovito doseganje blažilnih učinkov Si potrebna s pojavom stresnih simptomov sočasna zadostna preskrba rastlin s Si (Cooke in Leishman 2011a).

Znano je, da se je sposobnost aktivnega kopičenja Si v rastlinah pojavila večkrat neodvisno tekom evolucije, iz česar lahko sklepamo na konvergenten razvoj rabe Si pri rastlinah. Pravih vzročnih in časovnih povezav med temi dogodki zaenkrat še ne poznamo (Strömberg in sod. 2016). Večkraten neodvisen pojav sposobnosti aktivnega kopičenja Si v rastlinah podpira raziskava, ki so jo opravili Trembath-Reichert in sod. (2015). Ugotovili so, da sta visoka vsebnost Si ter prisotnost prenašalcev Si značilni tako za evolucijsko stare (mahovi in praprotnice) kot tudi najmlajše kopenske taksone rastlin (predvsem trave). Golosemenke, ki so razmah doživele vmes, večinoma zaznamujejo majhne količine Si ter redka pogostost pojavljanja prenašalcev Si. Iz tega lahko sklepamo na izgubo sposobnosti aktivnega kopičenja Si pri zadnjem skupnem predniku semenk ter njen ponoven kasnejši pojav pri kritosemenkah (Trembath-Reichert in sod. 2015). Najnovejše molekularne analize so hkrati razkrile tudi široko razširjenost procesa biosilicifikacije znotraj kopenskih rastlin in s tem pokazale na prvobitnost tega procesa pri kopenskih rastlinah (Trembath-Reichert in sod. 2015, Marron in sod. 2016) ter posledično na izreden pomen Si za metabolizem rastlin tudi pri linijah, kjer se ta ne pojavlja v znatnih količinah predvsem z namenom mehanske opore (Marron in sod. 2016). Trembath-Reichert in sod. 2015 so vsesplošno razširjenost procesa biosilicifikacije pri kopenskih rastlinah ugotovili predvsem na podlagi analize vsebnosti Si pri različnih taksonih, Marron in sod. (2016) pa so ta pojav povezali med drugim s sprva prav tako široko razširjenostjo Lsi2 podobnih prenašalcev Si. Ti naj bi se razvili z namenom razstrupljanja previsokih koncentracij Si v predkambriju in kasneje pri večini linij kopenskih rastlin zaradi splošnega upada njegove koncentracije izginili (Marron in sod. 2016).

Lastnost aktivnega kopičenja Si pri rastlinah naj bi postala pogostejša v pozni kredi (Katz 2015). Kot omenjeno že v prvem poglavju, trave so v splošnem znane po visoki vsebnosti Si (Ma in Takahashi 2002). Njihov izvor je vezan na zgodnji terciar, in sicer paleocen. Razmah so najprej doživele C_3 trave, v srednjem miocenu pa so se razvile C_4 trave, ki naj bi se močno razširile v poznem miocenu na račun upada koncentracije atmosferskega CO_2 zaradi večje tolerance do nižje koncentracije CO_2 v primerjavi s C_3 travami (Jacobs in sod. 1999). Osborne (2008) je idejo o razmahu C_4 trav na račun upada koncentracije CO_2 postavil pod vprašaj, saj je med obdobjem največjega upada koncentracije CO_2 ter pojava prvih C_4 rastlin kar okoli 10 milijonov let razlike. Njihovo širjenje v tem obdobju bi lahko povezali tudi s povečanjem sezonskosti padavinskega režima ter frekvence pojavljanja požarov (Osborne 2008). Dejstvo pa je, da je z upadom CO_2 močno pridobila na pomenu sposobnost trav za kopičenje večjih količin Si (Cooke in Leishman 2011a). McNaughton in Tarrants (1983) ter McNaughton in sod. (1985) so na podlagi izmerjenih višjih koncentracij Si pri objedenih listih prišli do zaključka, da bi silicifikacija lahko predstavljala inducirano zaščito trav pred objedanjem rastlinojedih sesalcev in s tem igrala pomembno vlogo pri koevoluciji med travami ter rastlinojedimi sesalci. Podobno sta razmišljala tudi Stebbins (1981) ter Katz (2015). Pravkar omenjeni koevolucijski odnos med travami in rastlinojedimi sesalci bi torej lahko deloval kot ena od gonilnih sil za povečanje stopnje silicifikacije pri travah tekom evolucije (McNaughton in sod. 1985). Nekoliko drugačne rezultate so objavili Cid in sod. (1989), ki so pri objedenih rastlinah zaznali nižje koncentracije Si. To opažanje so razložili na osnovi nižje povprečne starosti listov in s tem manj razpoložljivega časa za njihovo silicifikacijo. Na ta način so omajali idejo o silicifikaciji kot inducibilnem tipu zaščite pred rastlinojedi. Pri neobjedenih rastlinah so sicer v splošnem višjo koncentracijo Si zaznali pri rastlinah iz objedanju izpostavljenih populacij v primerjavi s tistimi iz neizpostavljenih populacij, kar so pripisali razlikam v mikroklimi ter določenim morfološkim prilagoditvam rastlin iz objedanju izpostavljenih populacij (Cid in sod. 1989).

Vloga silicija pri rastlinah

Silicij rastlinam nudi številne koristi. Pomemben je za uspešno rast vseh rastlin, vendar njegov doprinos k njihovemu uspevanju pride do izraza šele v stresnih razmerah, saj ga v ugodnih razmerah v zadostnih količinah lahko pridobijo že iz tal (Ma 1990, Ma in Takahashi 2002). Rastline v različnih stresnih razmerah imajo ob prisotnosti Si višjo stopnjo fotosintezne aktivnosti ter nižjo stopnjo transpiracije v primerjavi z rastlinami v tovrstnih razmerah v odsotnosti Si, kar skupaj pripomore k povečani tvorbi suhe mase in hkrati tudi večji odpornosti teh rastlin na različne abiotske in biotske stresne dejavnike (Ma in Takahashi 2002). Poleg tega se z vključevanjem Si v rastlinska tkiva poveča tudi njihova trdnost (Adatia in Besford 1986, Ma in sod. 2001b, Hattori in sod. 2003), kar preprečuje poleganje in lomljenje stebel ob močnih vetrovih (Ma in sod. 2001b). Pri Si je za razliko od esencialnih elementov mehanska vloga bolj poudarjena od fiziološke. Koristi Si za rastline namreč večinoma izhajajo iz njegovega kopičenja v listih, steblih in semenskih ovojnicah (Ma in Takahashi 2002). Vseeno pa je znano, da Si spodbuja rast in razvoj rastlin ter pomaga blažiti stresne razmere tudi preko fizioloških mehanizmov, npr. s spodbujanjem metabolizma fenolnih snovi in izboljšanjem antioksidativnega potenciala rastlin (Ribera-Fonseca in sod. 2018), ter preko genske regulacije (Frew in sod. 2018).

Pomen silicija za rast in pogosti simptomi ob njegovem pomanjkanju

Dobro je dokumentiran spodbujajoč učinek Si na rast in uspevanje rastlin. Povečuje se skladno z naraščajočo koncentracijo Si in je bolj opazen pri rastlinah, ki so ga sposobne kopičiti več. Ogromno raziskav o koristnih učinkih Si na uspevanje rastlin je zato vezanih na akumulatorje Si (npr. riž). Na ta način je namreč lažje zaznati razliko med testnimi rastlinami, gojenimi ob prisotnosti Si ter testnimi rastlinami, ki rastejo ob pomanjkanju Si. Raziskave učinka Si na rast rastlin največkrat potekajo na osnovi vodnih kultur, saj je odstranjevanje Si iz medija na ta način najbolj enostavno. Koncentracija Si v rastlinskih tkivih se običajno tekom življenja rastlin povečuje (Ma in Takahashi 2002, Zhang in sod. 2013a, Grašič in sod. 2019c), zato je razlika v prirastu rastlin ob prisotnosti in odsotnosti Si bolj očitna v reproduktivni kot v vegetativni fazi (Ma in sod. 1989). Mnogi raziskovalci so opisali številne simptome ob pomanjkanju Si pri rastlinah. Opisani simptomi vključujejo upad suhe mase poganjkov, zmanjšanje pridelka, pojav nekroz in kloroz, zvijanje, otrdevanje, odebelitev, sušenje, povešanje in venenje listov, večjo podvrženost različnim boleznim, motnje pri oprašitvi in razvoju plodov ter pospešeno senescenco. Tovrstne raziskave se večinoma nanašajo na riž, kumaro, paradižnik, sojo, jagodo in preslice (Mitsui in Takatoh 1963, Chen in Lewin 1969, Miyake in Takahashi 1978, 1983a,b, 1985, Adatia in Besford 1986, Miyake in Takahashi 1986, Marschner in sod. 1990, Ma in Takahashi 2002). Preslice ob dolgoročnem pomanjkanju Si lahko celo dokončno propadejo (Chen in Lewin 1969). Simptomi pomanjkanja se velikokrat pokažejo šele v fazi cvetenja ob razvoju prvega cvetnega popka (Miyake in Takahashi 1978, 1983a, Ma in Takahashi 2002), kar nakazuje potencialen vpliv Si na hormone, ki nadzorujejo razvoj rastlin (Ma in Takahashi 2002). Običajno se simptomi najprej izrazijo na starejših listih in sčasoma napredujejo k mlajšim listom (Chen in Lewin 1969, Miyake in Takahashi 1978, 1983a,b, Adatia in Besford 1986). Pri rastlinah, od vsega začetka gojenih ob pomanjkanju Si, se simptomi pomanjkanja s kasnejšim dodatkom Si omilijo. Kadar rastline pomanjkanju Si izpostavimo v kasnejši fazi, se simptomi njegovega pomanjkanja pojavijo le na novih listih (Miyake in Takahashi 1978, 1983a).

Fotosintezna aktivnost

Nalaganje Si v listih pomaga pri vzdrževanju listov v pokončnem položaju, s čimer se zmanjša stopnja senčenja v gostih sestojih ter izboljša učinkovitost rabe svetlobe pri rastlinah. Oba učinka v končni fazi prispevata k višji stopnji fotosintezne aktivnosti (Ma in Takahashi 2002). Si strukture v listih naj bi služile kot nekakšna okna za lažje prehajanje svetlobe skozi list in s tem omogočale boljšo rabo svetlobe ter posledično večjo fotosintezno aktivnost, vendar Agarie in sod. (1996) pri listih riža tega niso dokazali. Si lahko spodbujajoče vpliva na proces fotosinteze tudi preko povečanja stopnje asimililacije CO_2 (Ma in Takahashi 2002). Sposobnost povečanja fotosintezne aktivnosti na račun Si lahko prispeva k zadostni oskrbi rastlin s snovjo in energijo za premagovanje različnih stresnih dejavnikov, ki negativno vplivajo na njihovo uspevanje (Zuccarini 2008, Shen in sod. 2010b, Nezami in Bybordi 2011, Ali in sod. 2013, Bharwana in sod. 2013, Rios in sod. 2014, Sanglard in sod. 2014, Shen in sod. 2014a, Song in sod. 2014, Mihaličová Malčovská in sod. 2014b, Maghsoudi in sod. 2015, Rodrigues in sod. 2015, Maghsoudi in sod. 2016, Qin in sod. 2016, Tripathi in sod. 2017).

Zaščita pred sušo

Zmanjšana fotosintezna aktivnost je med drugim lahko povezana s povečano stopnjo izgube vode oz. transpiracije, saj ta privede do zapiranja listnih rež, ki igrajo pomembno vlogo pri fotosintezi (Ma in Takahashi 2002). Suša ima negativen vpliv na rast in fotosintezno aktivnost tudi v smislu zniževanja vsebnosti klorofila in vpliva na celovitost tilakoidnih membran kloroplastov ter zmanjševanja učinkovitosti rastlin za rabo svetlobe. Vse naštete simptome rastline lahko rešujejo s pomočjo Si (Maghsoudi in sod. 2015, Ma in sod. 2016, Madi in Al-Mayahi 2016, Ouzounidou in sod. 2016). Ta zmanjša negativne posledice suše na njihovo uspevanje predvsem na račun višje stopnje fotosintezne aktivnosti preko različnih mehanizmov za izboljšanje relativne vsebnosti vode v rastlini (Gong in sod. 2003, Ma in sod. 2004a, Hattori in sod. 2005, Ahmed in sod. 2011a, Habibi in Hajiboland 2013, Habibi 2014, Saud in sod. 2014, Amin in sod. 2016, Maghsoudi in sod. 2016). Transpiracija ne poteka le skozi listne reže, temveč deloma tudi skozi kutikulo (Ma in Takahashi 2002). Učinek transpiracije skozi kutikulo se lahko zmanjša zaradi povečanega nalaganja voskov nad kutikulo ob dodatku Si (Madi in Al-Mayahi 2016), ali pa neposredno z nalaganjem Si pod kutikulo, kjer Si ustvari dodatno plast za zaščito pred izgubo vode (Yoshida in sod. 1962b, Postek 1981, Davis 1987, Ma in Takahashi 2002, Ma 2004). Podobno funkcijo Si opravlja tudi v koreninah, kjer spodbuja podaljševanje korenin in krepi celične stene v endodermisu ter preprečuje izgubo vode iz korenin v primeru nižjega vodnega potenciala tal in na ta način deluje kot mehanska in fiziološka ovira (Hattori in sod. 2003, Lux in sod. 2002). Si blaži učinek suše tudi na ta način, da poveča ksilemski vodni potencial (Marques in sod. 2016). Z nalaganjem Si na različnih mestih si rastline v splošnem izboljšajo svojo zadrževalno sposobnost za vodo in hkrati optimizirajo učinkovitost rabe vode (Gao in sod. 2004, Ma in sod. 2004a, Eneji in sod. 2005, Ahmed in sod. 2011b, Janislampi 2012, Kurdali in sod. 2013, Ouzounidou in sod. 2016). Dodatni opisani učinki Si ob pomanjkanju vode so povečanje prevodnosti listnih rež (Silva in sod. 2012, Habibi in Hajiboland 2013) ter zmanjšanje njihove gostote (Putra in sod. 2015), odebelitev povrhnjice (Asmar in sod. 2013), izboljšanje hidravlične prevodnosti korenin (Shi in sod. 2016) ter uravnavanje privzema vode preko povečanega izražanja določenih genov, ki kodirajo akvaporine oz. vodne kanalčke (Liu in sod. 2014) ali preko povečanega izražanja določenih transkripcijskih faktorjev za odziv ob suši (Khattab in sod. 2014). Poročali so tudi o njegovi vlogi pri osmotski regulaciji, ki je vidna na podlagi spremembe koncentracije osmotskih regulatorjev, kot so npr. prolin in topni sladkorji (Kaya in sod. 2006, Gunes in sod. 2008, Crusciol in sod. 2009, Sonobe in sod. 2010, Shen in sod. 2010b, Tale Ahmad in Haddad 2011, Pereira in sod. 2013, Khattab in sod. 2014, Karmollachaab in Gharineh 2015, Madi in Al-Mayahi 2016, Mauad in sod. 2016) ter pri uspevanju kserofitov z visoko vsebnostjo Na^+ (Kang in sod. 2014) in nadalje o zakasnitvi senescence v sušnih razmerah (Ouzounidou in sod. 2016, Hosseini in sod. 2017) preko uravnavanja razmerja med poliamini in etilenom (Yin in sod. 2014), izboljšani rasti ob suši na račun povišanja koncentracij ustreznih rastlinskih hormonov (Hamayun in sod. 2010, Abdalla 2011), povečanju trdnosti tkiv v listih in plodovih (Ouzounidou in sod. 2016) in s tem zmanjšanju prepustnosti membran (Agarie in sod. 1998) ter izboljšanem uspevanju v sušnih razmerah zaradi povečanja antioksidativne sposobnosti (Ma in sod. 2004a, Gong in sod. 2005, 2008, Gunes in sod. 2008, Pei in sod. 2010, Abdalla 2011, Habibi in Hajiboland 2013, Emam in sod. 2014, Habibi 2014, Shi in sod. 2014, 2015a, Jafari in sod. 2015, Ma in sod. 2016, Madi in Al-Mayahi 2016, Ouzounidou in sod. 2016, Shi in sod. 2016). Pozitiven učinek Si v sušnih razmerah ni zaznaven le na ravni odraslih rastlin, temveč tudi v fazi kalitve (Hameed in sod. 2013, Shi in sod. 2014).

Zmanjševanje škodljivih učinkov povišane slanosti

Povišana slanost tal ima na rastline vsaj v začetni fazi zelo podoben učinek kot suša, saj prav tako omejuje privzem vode v rastline (Munns 2002). Posledično so tudi mehanizmi Si za izboljšanje uspevanja rastlin pri povišanih koncentracijah soli podobni kot v primeru suše (Tripathi in sod. 2017). V splošnem se v njegovi prisotnosti poveča relativna vsebnost vode, s čimer pride do učinka redčenja soli v tkivih, optimizacije transpiracije in prevodnosti rež ter v končni fazi izboljšanja fotosintezne aktivnosti (Romero-Aranda in sod. 2006, Reezi in sod. 2009, Haghighi in Pessarakli 2013, Rohanipoor in sod. 2013, Muneer in sod. 2014, Liu in sod. 2015, Ouzounidou in sod. 2016). Ob presežku soli, ki zavira rast rastlin, Si pomaga ohranjati celovitost celičnih membran (Hashemi in sod. 2010, Qados 2015, Ouzounidou in sod. 2016) ter omejuje privzem in prenos natrija (Na) in s tem ublaži negativen vpliv povišane slanosti (Matoh in sod. 1986, Ahmad in sod. 1992, Liang 1999, Zhao in sod. 2007, Saqib in sod. 2008, Zuccarini 2008, Hashemi in sod. 2010, Farshidi in sod. 2012, Batool in sod. 2015, Mahdieh in sod. 2015, Li in sod. 2016, Yin in sod. 2016, Garg in Bhandari 2016b). Zhao in sod. (2007) ter Yin in sod. (2016) zmanjšan privzem in prenos Na ob dodatku Si pripisujejo njegovemu vplivu na aktivnost nekaterih ionskih kanalčkov preko povišanja koncentracije poliaminov, Ahmad in sod. (1992) pa njegovi sposobnosti za vezavo z Na. Poročali so tudi o hkratnem zmanjšanju privzema Na ter povečanju privzema K ob dodatku Si (Liang in sod. 1996, Liang in Ding 2002, Tahir in sod. 2007, Levent Tuna in sod. 2008, Ali in sod. 2009, Ashraf in sod. 2009, 2010, Farooq in sod. 2015, Ghassemi-Golezani in Lotfi 2015, Khan in sod. 2015, Xu in sod. 2015), oz. o povečanju razmerja K^+/Na^+ kljub naraščajoči koncentraciji Na^+ (Gengmao in sod. 2015). Liang in sod. (1996) ter Levent Tuna in sod. (2008) so upad koncentracije Na povezali s sposobnostjo Si za zmanjšanje prepustnosti membran. Povečanje razmerja K^+/Na^+ bi bilo lahko tudi rezultat vpliva Si na povečano izražanje genov, ki kodirajo K kanalčke (Muneer in Jeong 2015). Dodatek Si se kaže tudi v povečanem privzemu Ca (Levent Tuna in sod. 2008, Habibi in sod. 2014, Garg in Bhandari 2016a), Mg (Garg in Bhandari 2016b), Fe in cinka (Zn) (Batool in sod. 2015) ter privzemu in prenosu N iz korenin v poganjke in povečanju aktivnosti encimov za razstrupljanje amonijaka (Kochanová in sod. 2014, Tantawy in sod. 2015, Mahdavi in sod. 2016, Garg in Bhandari 2016b). Številni raziskovalci so poudarili pomen Si za učinkovitejše delovanje antioksidativnih mehanizmov pri povišanih koncentracijah soli (Liang 1999, Liang in sod. 2003, Al-Aghabary in sod. 2004, Zhu in sod. 2004, Moussa 2006, Saqib in sod. 2008, Reezi in sod. 2009, Hashemi in sod. 2010, Tale Ahmad in Haddad 2011, Ali in sod. 2012, Farshidi in sod. 2012, Kim in sod. 2014b, Farooq in sod. 2015, Gengmao in sod. 2015, Liu in sod. 2015, Qados 2015, Zhang in sod. 2015, Bybordi 2016, Garg in Bhandari 2016a, Li in sod. 2016, Ouzounidou in sod. 2016). O ugodnih vplivih Si na uspevanje rastlin ob povišani slanosti so poročali tudi Yeo in sod. (1999), ki so kot vzrok izboljšanja njihove rasti navedli omejevanje transpiracijskega toka na račun odlaganja Si v endodermisu in najbolj zunanji plasti korenin ter njegove polimerizacije v apoplastu korenin. Do podobnih zaključkov so prišli tudi Gong in sod. (2006) ter Savvas in sod. (2007, 2009). Si privzem vode ob povišani slanosti izboljša tudi preko povečanega izražanja nekaterih genov, ki kodirajo akvaporine (Liu in sod. 2015), ali spodbujanja aktivnosti H^+-ATPaz ter H^+-PPaz, ki omogočijo prenos in shranjevanje Na v vakuolah skozi Na^+/H^+ antiporterje na tonoplastu vakuol (Liang in sod. 2005c, 2006b, Xu in sod. 2015). Almutairi (2016) je poročal o povečanju tolerance rastlin do povišane slanosti na podlagi spremembe izražanja različnih genov ob dodatku Si. Nekateri raziskovalci so izboljšanje uspevanja rastlin ob dodatku Si v razmerah s povišano slanostjo povezali z njegovo vlogo pri uravnavanju koncentracij rastlinskih hormonov (Hamayun in sod. 2010, Lee in sod. 2010). Zaščito pred povišano slanostjo Si prav tako kot v primeru suše nudi s povečanjem trdnosti tkiv (Stamatakis in sod. 2003, Ouzounidou in sod. 2016) in s tem zakasnitvijo procesa senescence (Ouzounidou in sod. 2016). Podobno lahko Si tudi ob povišani slanosti igra pomembno vlogo pri osmotski regulaciji preko uravnavanja koncentracije osmotskih regulatorjev, kot so npr. prolin ter različni topni sladkorji (Levent Tuna in sod. 2008, Yin in sod. 2013, Kalteh in sod. 2014, Abbas in sod. 2015, Zhang in sod. 2015, Abdel Latef in Tran 2016, Qin in sod. 2016). Tudi v primeru povišane slanosti se pozitiven učinek Si kaže tako v fazi kalitve kot pri kasnejših razvojnih fazah (Solatni in sod. 2012, Sabaghnia in Janmohammadi 2014, Khan in sod. 2015, Almutairi 2016), vsaj kadar gre za nizke koncentracije Si (Zhang in sod. 2015).

Vloga pri povečani stopnji UV sevanja

Povečana stopnja UV sevanja pri rastlinah povzroča poškodbe tako na ravni celotne rastline v smislu negativnega vpliva na rast in produktivnost (Lizana in sod. 2009, Shen in sod. 2010a,b), kot na ravni DNA (kar se lahko z dednimi mutacijami prenaša v naslednje generacije) ter fizioloških procesov (Stapleton 1992), kar se kaže v tvorbi strupenih reaktivnih kisikovih zvrsti (v nadaljevanju ROS) in posledično pojavu oksidativnega stresa (Mackerness 2000, Yao in sod. 2011). Do danes se je nabralo že lepo število raziskav, ki Si pripisujejo pomembno vlogo pri povečanju tolerance rastlin do visoke jakosti UV sevanja, vidne na podlagi višje stopnje fotosintezne aktivnosti in nižje stopnje transpiracije (Shen in sod. 2010b, Yao in sod. 2011, Shen in sod. 2014a), povečane antioksidativne sposobnosti (Yao in sod. 2011, Shen in sod. 2014a, Chen in sod. 2016) ali nižje koncentracije tako škodljivih ROS kot tudi zaščitnih fenolnih substanc (Goto in sod. 2003, Shen in sod. 2010a,b, Mihaličová Malčovská in sod. 2014a). Na podlagi obratno sorazmernega odnosa med količino nakopičenega Si v rastlinskih tkivih pri povečani stopnji UV sevanja ter količino zaščitnih fenolnih snovi lahko sklepamo, da Si rastlinam nudi enako zaščito kot z vidika izgradnje energetsko bolj potratne fenolne snovi (Schaller in sod. 2012, 2013). Li in sod. (2004) ter Chen in sod. (2016) so v nasprotju s prej omenjenimi raziskavami pri rastlinah, izpostavljenih povečani stopnji UV sevanja, ob dodatku Si zaznali porast koncentracije zaščitnih fenolnih UV-absorbirajočih snovi. Zelo pomembno zaščitno vlogo pred povečano stopnjo UV sevanja imajo tudi Si strukture v kutikuli, laskih in povrhnjici listov, saj povečajo odboj UV dela svetlobnega spektra ter razpršijo sevanje vidnega dela svetlobnega spektra, s čimer zmanjšajo prodiranje UV sevanja v globlja tkiva in tako vplivajo na notranji svetlobni gradient (Goto in sod. 2003, Schaller in sod. 2013, Klančnik in sod. 2014a,b). Zaščito v smislu optičnih lastnosti Si v listih predstavlja tudi na podlagi majhne stopnje absorpcije v UV delu spektra (Goto in sod. 2003, Fang in sod. 2006). Kljub vsemu še vedno ni popolnoma jasno, ali se je vloga Si pri krojenju optičnih lastnosti listov tekom evolucije razvila z namenom aktivne zaščite, ali pa gre le za stranski učinek njegovega kopičenja v listih (Schaller in sod. 2013). Še eden od mehanizmov rastlin za povečanje tolerance do povečane stopnje UV sevanja s pomočjo Si je povezan z izražanjem gena *Lsi1*, ki kodira prenašalce za privzem Si v rastline (Ma in Yamaji 2008). Povečano izražanje tega gena se ne kaže le v povečanem privzemu Si, temveč omogoči tudi povečano izražanje nekaterih za toleranco rastlin do povečane stopnje UV sevanja pomembnih genov, vpletenih tako pri popravljanju fotopoškodb kot tudi pri fotosintezi in razstrupljanju (Fang in sod. 2011a,b, Chen in sod. 2016).

Blaženje stresa zaradi ekstremnih temperatur

Previsoke temperature škodljivo vplivajo na rast, metabolizem in produktivnost rastlin, saj privedejo do oksidativnega stresa in s tem povišane stopnje tvorbe ROS, poškodb celic in membran, zmanjšane stopnje fotosintezne aktivnosti in še mnogih drugih učinkov (Ruelland in Zachowski 2010, Tan in sod. 2011, Hasanuzzaman in sod. 2013). Wang in sod. (2005) so v svoji raziskavi predstavili možnost učinkovitega ohlajanja pregretih listov preko oddajanja sevanja v srednjevalovnem infrardečem spektru zaradi Si struktur v povrhnjici listov. Si naj bi hkrati omogočal tudi hlajenje korenin (Wang in sod. 2005). Björn in Li (2011) nasprotno nista zaznala večjih razlik med oddanim sevanjem pri listih s Si revnih ter s Si bogatih rastlin in ovrgla to možnost ohlajanja listov. Agarie in sod. (1998) so Si pripisali vlogo pri ohranjanju stabilnosti maščob v celičnih membranah ob visokih temperaturah in s tem ohranjanju celovitosti celičnih membran. Dodatek Si omogoča boljšo rast rastlin ob visokih temperaturah na račun povečanja vsebnosti proteinov, ki domnevno izboljšajo odpornost rastlin na visoke temperature, ter povečanja stopnje aktivnosti nekaterih antioksidativnih encimov (Soundararajan in sod. 2014). Omili se tudi učinek zmanjšane plodnosti zaradi previsokih temperatur na račun povečane kakovosti peloda (Wu in sod. 2014).

Ekstremno nizke temperature prav tako omejujejo uspevanje rastlin, saj med drugim povzročajo oksidativni stres, kloroze, nekroze, zavirajo rast, zmanjšajo vsebnost vode v tkivih, stopnjo fotosintezne aktivnosti ter učinkovitost rabe vode (Steponkus 1984, Zhu in sod. 2006, Liang in sod. 2008, Sanghera in sod. 2011). Glavni mehanizem Si za povečano toleranco rastlin proti mrazu je vezan na povečanje stopnje antioksidativne zaščite preko izboljšanja sposobnosti rastlin za zadrževanje vode, kar pozitivno vpliva na njihovo stopnjo rasti in sposobnost ohranjanja stabilnosti in celovitosti celičnih membran (Liang in sod. 2008, Liu in sod. 2009b, Habibi 2015b, 2016). Zaščito pred ekstremno nizkimi temperaturami Si rastlinam nudi tudi na račun povečane trdnosti celičnih sten in s tem oviranja nastanka ledenih kristalov (Larcher in sod. 1991). Sivanesan in sod. (2014) so ugotovili, da fotokemična učinkovitost rastlin, izpostavljenih nižjim ali višjim temperaturam, ob dodatku Si ne upade bistveno v primerjavi z rastlinami, rastočimi pri običajnih temperaturah. Na podlagi tega so zaključili, da Si pri rastlinah ob temperaturnem stresu omogoča normalno delovanje fotosinteznega aparata (Sivanesan in sod. 2014).

Vpliv silicija na uravnavanje neravnovesja nekaterih pomembnejših hranil

V različnih stresnih razmerah, kot so npr. povečana slanost tal, pomanjkanje vode ali ekstremne temperature, se pogosto poruši tudi ravnovesje hranil v rastlinah. To vodi v osmotski in oksidativni stres ter v končni fazi celo do propada rastlin (Tripathi in sod. 2017). Uravnavanje neravnovesja hranil je še eden od mnogih pomembnih vidikov Si (Neu in sod. 2017, Greger in sod. 2018), ki pripomore k boljšemu uspevanju rastlin.

Dušik (N)

Prenizka koncentracija N v rastlinah povzroči upad fotosintezne aktivnosti ter rasti celic, s čimer v končni fazi zavira rast listov (Fallah 2012). Pride tudi do kloroz, nekroz in celo propada rastlin (Hartz in sod. 2009). Eden izmed možnih virov N za rastline ob premagovanju stresnih razmer je prolin (Fukutoku in Yamada 1984), katerega koncentracija se ob dodatku Si poveča (Crusciol in sod. 2009, Shahnaz in sod. 2011). Obstaja nemalo raziskav, ki vsaj do določene mere kažejo na pozitiven učinek dodajanja Si na metabolizem N (Watanabe in sod. 2001, Mali in Aery 2008b, Kurdali in sod. 2013, Pereira in sod. 2013, Kochanová in sod. 2014, Castro de Souza in sod. 2016). Si ima na koncentracijo N lahko tudi obraten vpliv. Deren (1997) je v svoji raziskavi ob zadostnih koncentracijah N poročal o zniževanju koncentracije N z dodajanjem Si. Ob prisotnosti Si se rastlinam poviša prag optimalne vsebnosti N, zaradi česar se ob močno povišani koncentraciji N njihov prirast lahko še vedno povečuje v primerjavi z rastlinami, ki rastejo v enakih razmerah, a ob odsotnosti Si. Slednjim se namreč ob izredno visokih koncentracijah N listi pričnejo povešati, s čimer lahko pride do medsebojnega senčenja in posledično zmanjšane fotosintezne aktivnosti. Takšne rastline postanejo tudi bolj dovzetne za različne okužbe (Ma in Takahashi 2002). Si k izboljšanju uspevanja rastlin s povešenimi listi zaradi presežka N lahko prispeva tudi na račun povečanja trdnosti in s tem vzdrževanja listov v bolj pokončnem položaju (Yoshida in sod. 1969, Idris in sod. 1975).

Fosfor (P)

Pozitivni učinki Si se pokažejo tudi ob pomanjkanju P. Tipični znaki njegovega pomanjkanja so zavrta rast in zapoznelo dozorevanje ter vijolična obarvanost listov (Uchida 2000). Ob vnosu Si v tla z nezadostno količino P se poveča pridelek rastlin, saj Si zmanjša njihovo potrebo po P (Roy in sod. 1971). Ma in Takahashi (2002) sta prišla do podobnega zaključka z ugotovitvijo, da se ob dodajanju Si pri pomanjkanju P poveča suha masa poganjkov. Pri nižjih koncentracijah P je učinek Si večji. P ima visoko afiniteto do kovin, kot sta Fe in Mn. Ob nizkih koncentracijah P ti dve kovini vplivata na njegov privzem (Ma in Takahashi 2002). Do pozitivnega učinka Si na rast ob pomanjkanju P pride na račun izboljšanja dostopnosti P znotraj samih rastlin na račun zmanjšanja privzema Mn in Fe ter s tem povišanja razmerja P/Mn in P/Fe v rastlinah (Ma in Takahashi 1990a,b, 1991). Deren (1997) je poročal o povišanju koncentracije P v rastlinah na račun gnojenja s Si ob pomanjkanju P, Cheong in Chan (1973) pa sta ob dodatku Si zaznala povišano stopnjo fosforilacije in s tem tvorbe organskih P spojin, kar se je navzven odražalo v povečani stopnji rasti. Khalid in Silva (1980) sta ugotovila, da se ob dodatku Si nekoliko poviša dostopnost P v vrhnji plasti tal. Ta učinek je večinoma posledica vezave Si s Fe in Al, ki se sicer pogosto vežeta s P in s tem zmanjšujeta njegovo dostopnost (Roy 1969, Khalid in Silva 1980). Si je koristen tudi ob previsokih koncentracijah P, ki povzročajo različne kloroze na rastlinah. Z dodajanjem Si se namreč ob dolgoročni zadostni preskrbi rastlin s P, predvsem pa ob presežku P, zmanjšata stopnja njegovega privzema v rastline ter koncentracija v rastlinah preko odlaganja Si v koreninah in znižane stopnje transpiracije (Ma in Takahashi 1989, 1990a, Marschner in sod. 1990, Ma in Takahashi 2002).

Kalij (K)

Pomanjkanje K se pri rastlinah kaže predvsem skozi nekroze na robovih in končnih delih listov (Joiner in sod. 1983), negativen vpliv na vodni režim in transport po rastlini ter zmanjšano stopnjo fotosintezne aktivnosti in s tem prirast (Zhao in sod. 2001, Pettigrew 2008, Gerardeaux in sod. 2010). Ob visokih koncentracijah NaCl se običajno poveča prepustnost celičnih membran, posledica česar je med drugim tudi znižana koncentracija K v rastlinah (Liang in sod. 1996, Ashraf in sod. 2009). Si v tovrstnih razmerah zmanjša prepustnost celičnih membran in izboljša sposobnost rastlin za privzem K (Liang in sod. 1996, Liang 1999, Kaya in sod. 2006, Mali in Aery 2008a, Levent Tuna in sod. 2008) ter s tem pomaga pri vzdrževanju zadostne koncentracije K v rastlinah (Liang in sod. 1996). Poleg povečanja koncentracije (Ashraf in sod. 2009, Miao in sod. 2010) in izboljšanja učinkovitosti rabe K ob njegovem pomanjkanju Si izboljša tudi antioksidativno aktivnost rastlin (Miao in sod. 2010).

Kalcij (Ca)

Nezadostna koncentracija Ca se navzven odraža preko nekroz (Marinos 1962, Simon 1978, Uchida 2000), na celični ravni pa negativno vpliva na celovitost in prepustnost celičnih membran (Marinos 1962, Poovaiah 1979). Ob zmanjšanju koncentracije Ca zaradi previsoke slanosti in posledični povečani prepustnosti celičnih membran Si poskrbi za ponovno zmanjšanje prepustnosti celičnih membran in s tem za ohranjanje njihove celovitosti (Liang in sod. 1996, Liang 1999, Levent Tuna in sod. 2008). Ugotovitve različnih raziskav glede vpliva Si na koncentracijo Ca v rastlinah se zelo razlikujejo, pri čemer tega vpliva ne moremo povezati z dostopnostjo Ca pred dodajanjem Si. Liang (1999) namreč ob pomanjkanju Ca ni zaznal bistvenega vpliva Si na koncentracijo Ca v rastlinah, Ma in Takahashi (1993) ter Brackhage in sod. (2013) so poročali o nižanju koncentracije Ca na račun višanja koncentracije Si, medtem ko se je v nekaterih raziskavah koncentracija Ca vsaj do določene mere povečevala z naraščajočo koncentracijo Si (Kaya in sod. 2006, Mali in Aery 2008a,b, Levent Tuna in sod. 2008), pri čemer je bila pri dveh od slednjih raziskav koncentracija Ca znižana na račun suše ali povišane slanosti (Kaya in sod. 2006, Levent Tuna in sod. 2008), v preostalih dveh pa normalna (Mali in Aery 2008a,b). Brackhage in sod. (2013) so zmanjševanje koncentracije Ca ob visoki razpoložljivosti Si povezali s strategijo rastlin za premagovanje stresa zaradi previsokih količin Ca ter z nadomeščanjem Ca kot strukturnega elementa z energetsko cenejšim Si.

Zmanjševanje negativnih učinkov različnih kovin

Toksične kovine za kulturne rastline glavno oviro predstavljajo z vidika zmanjševanja njihove produktivnosti. Prvi odziv rastlin se pokaže v tvorbi ROS, ki negativno vplivajo na njihov metabolizem (Yadav 2010). Do sedaj se je nabralo že veliko število raziskav o vlogi Si pri blaženju posledic zaradi toksičnih koncentracij vrste različnih kovin, ki so opisane v sledečih podpoglavjih (Preglednice 2–9). Pozitivni učinki Si se najpogosteje kažejo v zmanjšanju dostopnosti, privzema in prenosa kovin iz korenin v poganjke, njihovem odlaganju v celičnih stenah, povečanju elastičnosti in plastičnosti celičnih sten ter povečanju antioksidativne sposobnosti (Tripathi in sod. 2017).

Železo (Fe)

Povečana koncentracija Fe v obliki Fe^{2+} se na rastlinah v največji meri odraža v zavrti rasti, nekrozah in rjavenju (Snowden in Wheeler 1993, De Dorlodot in sod. 2005), zmanjšani vsebnosti vode in določenih hranil (Majerus in sod. 2007), pridelka (Sahrawat 2004), poškodbi membran in tvorbi ROS (Sinha in sod. 1997, Thongbai in Goodman 2000).

Aluminij (Al)

Pri nizkih pH vrednostih Al za rastline pogosto postane toksičen (Mossor-Pietraszewska 2001). Presežek Al^{3+} ionov omejuje rast korenin ter privzem hranil (Matsumoto 2000, Ma in Takahashi 2002; Panda in sod. 2009). Negativen vpliv previsokih koncentracij Al se pri rastlinah kaže tudi preko povečane tvorbe ROS, zaviranja procesa celičnega dihanja (Matsumoto 2000, Yamamoto in sod. 2002, Kao in Kuo 2003, Panda in sod. 2009), povečanja togosti tako celičnih sten kot DNA in posledično zmanjšanja stopnje podvajanja DNA (Foy 1992), oviranja prenosa znotraj rastlin zaradi povečanega kopičenja polisaharida kaloze v plazmodezmah ter motenj v strukturi citoskeleta (Matsumoto 2000, Panda in sod. 2009).

Preglednica 2: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij železa (Fe).
Table 2: The role of silicon (Si) in alleviation of negative effects caused by toxic iron (Fe) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Fe	Viri
povečanje oksidativne sposobnosti korenin z dovajanjem O iz poganjkov v korenine in s tem zmanjšan privzem zaradi oksidacije Fe^{2+} v Fe^{3+} na površini korenin	Ma in Takahashi (2002)
zmanjšanje koncentracije Fe preko zaviranja njegovega prenosa iz korenin v poganjke ter izboljšana antioksidativna zaščita	Chalmardi in sod. (2014)
zmanjšanje kopičenja in privzema Fe, povečanje prenosa Fe med koreninami in poganjki, odebelitev celičnih sten	Fu in sod. (2012)
zmanjšanje privzema Fe iz kislih tal preko povečanja sproščanja OH^- ionov iz korenin in s tem zvišanja pH tal	Wallace (1992)

Preglednica 3: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij aluminija (Al).
Table 3: The role of silicon (Si) in alleviation of negative effects caused by toxic aluminium (Al) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Al	Viri
povečanje koncentracije fenolnih snovi in prolina ter zmanjšanje stopnje lipidne peroksidacije	Shahnaz in sod. (2011)
povečana aktivnost antioksidativnih encimov, izboljšanje procesa fotosinteze	Shen in sod. (2014b)
povečana tvorba fenolnih snovi	Kidd in sod. (2001)
skupno obarjanje Al in Si, tvorba inertnih Al-Si kompleksov ter zmanjšan privzem Al	Galvez in Clark (1991), Barcelo in sod. (1993), Hodson in Sangster (1993), Baylis in sod. (1994), Corrales in sod. (1997), Ma in sod. (1997), Cocker in sod. (1998a), Rahman in sod. (1998), Cocker in sod. (1998b), Hodson in Sangster (1999), Vashegyi in sod. (2002), Ryder in sod. (2003), Wang in sod. (2004), Liang in sod. (2007), Prabagar in sod. (2011)
pozitiven učinek na rast, obnovitev koncentracije Ca v rastlinah ter zmanjšan privzem Al	Hammond in sod. (1995)
večja stopnja rasti na račun manjšega kopičenja Al ter vzdrževanja ravnovesja nekaterih hranil	Singh in sod. (2011)
zmanjšana dostopnost Al na podlagi zvišanja pH in s tem izboljšanje rasti rastlin	Galvez in sod. (1987), Li in sod. (1996)
znižanje koncentracije prostega oz. reaktivnega Al	Li in sod. (1989), Prabagar in sod. (2011)
zmanjšanje privzema Al iz kislih tal preko povečanja sproščanja OH^- ionov iz korenin in s tem zvišanja pH tal	Wallace (1992)
preprečevanje nastanka škodljivih polimeriziranih Al spojin	Lumsdon in Farmer (1995)

Liang in sod. (2001) ob dodatku Si pri zelo visokih koncentracijah Al niso opazili izboljšanja uspevanja rastlin, medtem ko je bil pri nekoliko nižjih, a še vedno previsokih koncentracijah Al pozitiven učinek Si na rast rastlin zaznaven. Blažilni učinek Si pri rastlinah ob toksičnih koncentracijah Al je najverjetneje odvisen od same vrste oz. kultivarja, koncentracije Al in trajanja stresa (Hodson in Evans 1995, Liang in sod. 2001) ter pH (Cocker in sod. 1997).

Mangan (Mn)

Presežek Mn v listih povzroči upad fotosintezne aktivnosti (Kitao in sod. 1997). Povišane koncentracije Mn se navzven kažejo v klorozi mladih listov, saj povzročijo pomanjkanje Fe, ki predstavlja pomemben člen v procesu izgradnje klorofila (Clairmont in sod. 1986). Pride tudi do pojava nekroz in poškodb korenin (Wu 1994, Foy in sod. 1995).

Jarvis in Jones (1987) za razliko od številnih ostalih raziskav učinka Si na Mn nista zaznala, v nekaterih drugih raziskavah pa so poročali le o delnem učinku Si v povezavi z Mn (Kluthcouski in Nelson 1980, Galvez in sod. 1987, 1989).

Svinec (Pb)

Povišane koncentracije svinca (Pb) vplivajo na zgradbo, rast in fotosintezno aktivnost rastlin, poleg tega pa spremenijo tudi encimsko aktivnost, vodni režim in ravnovesje hranil v rastlinah (Sharma in Dubey 2005).

Preglednica 4: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij mangana (Mn).
Table 4: The role of silicon (Si) in alleviation of negative effects caused by toxic manganese (Mn) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Mn	Viri
omejevanje privzema Mn v rastline preko povečanja oksidativne sposobnosti korenin za njegovo oksidacijo	Ma in Takahashi (2002)
povečana notranja toleranca do količine Mn v tkivih	Horiguchi (1988)
bolj enakomerno razporejanje Mn v listih v posledično nižjih in manj toksičnih koncentracijah	Williams in Vlamis (1957), Horst in Marschner (1978), Horiguchi in Morita (1987)
višja toleranca zaradi znižanja koncentracije in aktivnosti Mn^{2+} v apoplastu preko redoks reakcij	Horst in sod. (1999)
povečanje tolerance z vezavo Mn^{2+} v celične stene, znižanjem koncentracije Mn v simplastu ter vzdrževanjem reduciranega stanja apoplasta in s tem preprečevanjem oksidacije fenolnih snovi v apoplastu	Iwasaki in sod. (2002a), Iwasaki in sod. (2002b), Rogalla in Römheld (2002)
kopičenje Si skupaj z Mn na bazi trihomov in s tem omejevanje metabolne aktivnosti Mn	Iwasaki in Matsumara (1999)
povečana tvorba biomase, zmanjšana stopnja lipidne peroksidacije ter povečana antioksidativna sposobnost	Shi in sod. (2005a), Shi in Zhu (2008)
odebelitev povrhnjice in skladiščenje Mn v tkivih brez fotosintezne aktivnosti	Doncheva in sod. (2009)
zmanjšanje prenosa Mn iz korenin v poganjke	Shi in Zhu (2008)
izboljšanje fotosintezne aktivnosti ter spremenjeno izražanje genov, vpletenih pri procesu fotosinteze	Li in sod. (2015)

Kadmij (Cd)

Kadmij (Cd) je za večino rastlin toksičen že pri nizkih koncentracijah (Lux in sod. 2011). Njegov vpliv na rastline se kaže v zmanjšani fotosintezni aktivnosti ter znižani stopnji privzema vode in hranil, pride pa tudi do kloroz, nekroz, zavrte rasti in poškodb korenin (Kim in sod. 2003, Veselov in sod. 2003, Wójcik in Tukiendorf 2004, Wahid in sod. 2008, Lukačová Kuliková in Lux 2010).

Preglednica 5: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij svinca (Pb).
Table 5: The role of silicon (Si) in alleviation of negative effects caused by toxic lead (Pb) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Pb	**Viri**
izboljšana rast ter zmanjšan privzem Pb z vezavo Pb v tleh, omejevanjem njegovega prenosa iz korenin v poganjke in razstrupljanjem Pb ter večja aktivnost antioksidativnih encimov v koreninah	Li in sod. (2012), Bharwana in sod. (2013)
zmanjšan privzem Pb zaradi zmanjšanja njegove mobilnosti in dostopnosti v tleh	Yan in sod. (2014)

Preglednica 6: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij kadmija (Cd).
Table 6: The role of silicon (Si) in alleviation of negative effects caused by toxic cadmium (Cd) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Cd	**Viri**
zmanjšana koncentracija Cd, njegov privzem in prenos iz korenin v poganjke ter preprečevanje oksidativnih poškodb	Treder in Cieslinski (2005), Shi in sod. (2005b), Zhang in sod. (2008), Liu in sod. (2013), Zhang in sod. (2013b), Kim in sod. (2014a), Greger in Landberg (2015), Hussain et al. (2015), Tang in sod. (2015), Greger in sod. (2016)
povečana elastičnost in plastičnost celičnih sten	Vaculík in sod. (2009)
zmanjšana dostopnost v celicah poganjkov preko znižanja koncentracije v simplastu in povišanja v apoplastu	Vaculík in sod. (2012)
povečan razvoj apoplastnih barier in prevodnih tkiv v koreninah	Vaculík in sod. (2009, 2012), Vatehová in sod. (2012)
omejitev privzema in prenosa Cd v poganjke preko povečane tvorbe lignina in suberina v endodermisu	Vatehová in sod. (2012), Lukačová in sod. (2013)
povečana stopnja antioksidativne zaščite, izboljšana celovitost membran in zmanjšana koncentracija Cd	Song in sod. (2009), Shi in sod. (2010), Amiri in sod. (2012), Liu in sod. (2013), Lukačová in sod. (2013)
izboljšana fotosintezna aktivnost, metabolizem N in povečanje koncentracije prolina	Feng in sod. (2010), Mihaličová Malčovská in sod. (2014b), Hussain in sod. (2015)
izboljšana tvorba tilakoidnih membran v kloroplastih in s tem izboljšana fotosintezna aktivnost ter povečana tvorba biomase	Vaculík in sod. (2015)
povišana toleranca do Cd preko obarjanja Si v endodermisu in periciklu korenin	da Cunha in do Nascimento (2009)
zmanjšana koncentracija Cd preko vezave v celičnih stenah	Liu in sod. (2009a)
zmanjšana dostopnost in koncentracija Cd na račun zvišanja pH tal in s tem njegove vezave	Liang in sod. (2005b)
povečanje biomase rastlin in vezava Cd v različnih spojinah	da Cunha in sod. (2008)
uravnavanje metabolizma različnih proteinov ter uravnavanje izražanja genov, povezanih s Cd	Nwugo in Huerta (2011), Greger in sod. (2016)

Silicij izboljša uspevanje rastlin tudi v primeru pomanjkanja Cd, saj pripomore k boljši učinkovitosti rabe vode in svetlobe (Nwugo in Huerta 2008).

Cink (Zn)

Presežek Zn se pri rastlinah kaže predvsem v zaviranju rasti korenin in poganjkov ter pojavu kloroz na mladih listih (Ebbs in Kochian 1997). Zn je kemijsko zelo podoben Cd, zaradi česar med njima pogosto pride do tekmovanja za različna vezavna mesta tako na ravni tal kot rastlin (Christensen 1987, Christensen in Haung 1999, Welch in Norvell 1999, Zhao in sod. 2005). Povečana koncentracija Zn se posledično pogosto kaže v zmanjšanju koncentracije Cd, in obratno (Oliver in sod. 1994, Grant in Bailey 1997, Welch in Norvell 1999, Hart in sod. 2002, Zhao in sod. 2005, Grant in Sheppard 2008).

Silicij omogoča boljše uspevanje rastlin tudi v primeru nezadostne preskrbe s Zn, saj se z dodajanjem Si poveča dostopnost Zn (Marschner in sod. 1990). V dveh raziskavah učinka Si ob toksičnih koncentracijah Zn splošnega izboljšanja uspevanja rastlin niso zaznali (Masarovič in sod. 2012, Bokor in sod. 2014). Tvorba biomase ter antioksidativna sposobnost sta se v prisotnosti Si celo zmanjšali (Masarovič in sod. 2012), poleg tega pa so kljub zmanjšani koncentraciji Zn poročali tudi o povečanem fiziološkem stresu (Bokor in sod. 2014).

Baker (Cu)

Cu v presežku zavira rast rastlin ter povzroča nastanek kloroz (Yruela 2005), poleg tega pa negativno vpliva tudi na proces fotosinteze in povzroča oksidativni stres ter s tem nastanek škodljivih ROS (Sandmann in Böger 1980).

Preglednica 7: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij cinka (Zn).
Table 7: The role of silicon (Si) in alleviation of negative effects caused by toxic zinc (Zn) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Zn	Viri
povečanje biomase ter povečanje tolerance preko obarjanja Zn in Cd skupaj s Si v endodermisu in periciklu korenin	da Cunha in do Nascimento (2009)
izboljšana rast preko vzdrževanja ustrezne stopnje prepustnosti membran	Kaya in sod. (2009)
povečanje biomase rastlin in vezava Zn v različnih spojinah	da Cunha in sod. (2008)
začasna vezava Zn s Si v veziklih ali citoplazmi pred shranjevanjem Zn v vakuolah	Neumann in Zur Nieden (2001), Neumann in De Figueiredo (2002)
povečanje antioksidativne sposobnosti in ohranjanje celovitosti celičnih membran ter zmanjšan prenos Zn iz korenin v poganjke	Song in sod. (2011)
izboljšana fotosintezna aktivnost preko povečanega izražanja genov, vpletenih pri procesu fotosinteze	Song in sod. (2014)

Preglednica 8: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij bakra (Cu).
Table 8: The role of silicon (Si) in alleviation of negative effects caused by toxic copper (Cu) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Cu	Viri
povečanje biomase in vsebnosti vode ter zmanjšanje koncentracije Cu v poganjkih in koreninah	Nowakowski in Nowakowska (1997)
razstrupljanje Cu na račun njegove vezave v manj strupenih organskih in anorganskih CuS spojinah v poganjkih	Collin in sod. (2014)
povečana izgradnja molekul, ki vežejo Cu ter izražanje encimov, ki odstranjujejo ROS	Khandekar in Leisner (2011)
zmanjšanje negativnega učinka na rast in fotosintezni aparat preko preprečevanja prenosa Cu iz korenin v poganjke	Mateos-Naranjo in sod. (2015)
zmanjšana koncentracija in privzem Cu ter preprečevanje oksidativnih poškodb	Kim in sod. (2014a)
vzdrževanje ustreznih koncentracij različnih makro- in mikrohranil	Frantz in sod. (2011)

Krom (Cr)

Negativni učinki Cr se pri rastlinah kažejo na številnih fizioloških procesih. Zaradi preprečevanja izgradnje klorofila zavira proces fotosinteze (Vajpayee in sod. 2000), vpliva na vodni režim, ravnovesje hranil, zmanjšuje stopnjo rasti, povzroča kloroze in poškodbe koreninskega sistema (Sharma in sod. 2003, Gopal in sod. 2009, Truta in sod. 2014).

Preglednica 9: Vloga silicija (Si) pri blaženju učinkov toksičnih koncentracij kroma (Cr).
Table 9: The role of silicon (Si) in alleviation of negative effects caused by toxic chromium (Cr) concentrations.

Mehanizmi Si za blaženje simptomov toksičnosti Cr	Viri
znižana koncentracija Cr ter povečana stopnja rasti in fotosintezne aktivnosti	Tripathi in sod. (2015)
preprečevanje privzema in prenosa Cr ter izboljšana sposobnost zaščite pred oksidativnim stresom	Zeng in sod. (2011)
povečana stopnja rasti in fotosintezne aktivnosti preko razstrupljanja Cr	Ali in sod. (2013)

Zaščita pred škodljivimi učinki nekaterih drugih elementov

Arzen (As)

Škodljivi učinki As na rastline se kažejo tako na morfološki kot fiziološki ravni, in sicer preko zaviranja rasti korenin in poganjkov, zmanjšane fotosintezne aktivnosti, spremenjenega metabolizma ogljikovih hidratov in aminokislin ter pojava oksidativnega stresa (Hoffmann in Schenk 2011, Finnegan in Chen 2012, Tripathi in sod. 2012). Ob prisotnosti Si se zmanjša koncentracija As v rastlinah na račun omejevanja njegovega privzema (Guo in sod. 2005, 2007, Bogdan in Schenk 2008, Greger in sod. 2015, Greger in Landberg 2015, Suda in sod. 2016). Ta mehanizem temelji na tekmovanju med omenjenima elementoma (Guo in sod. 2009, Seyfferth in Fendorf 2012, Fleck in sod. 2013, Tripathi in sod. 2013). Kljub temu, da prenos Si in As poteka preko istih prenašalcev v celičnih membranah (Ma in sod. 2008), se elementa razlikujeta v vzorcu nalaganja znotraj celic (Moore in sod. 2011). Stopnja pozitivnega vpliva Si se lahko nekoliko razlikuje med različnimi kultivarji (Marmiroli in sod. 2014). Si ima pri rastlinah, izpostavljenih visokim koncentracijam As, pozitiven vpliv na razvoj korenin (Pandey in sod. 2016). Sanglard in sod. (2014) so poročali še o vlogi Si pri izboljšanju fotosintezne aktivnosti rastlin, Tripathi in sod. (2013) pa o njegovi sposobnosti povečanja antioksidativne sposobnosti in s tem zmanjšanja oksidativnega stresa rastlin, podvrženih toksičnim koncentracijam As.

Bor (B)

Presežek B zavira rast rastlin (Nable in sod. 1990a). Si lahko negativen vpliv previsokih koncentracij B na rastline blaži na več načinov, in sicer preko tvorbe kompleksov B-Si ter posledičnega zmanjšanja dostopnosti B (Gunes in sod. 2007a), zmanjšanja privzema B in povišanja tolerance do višjih koncentracij B v tkivih (Liang in Shen 1994, Inal in sod. 2009, Farooq in sod. 2015), omejevanja prenosa B iz korenin v poganjke (Gunes in sod. 2007a, Soylemezoglu in sod. 2009) in blaženja oksidativnega stresa zaradi previsokih koncentracij B (Gunes in sod. 2007a,b, Inal in sod. 2009, Soylemezoglu in sod. 2009, Kaya in sod. 2011, Farooq in sod. 2015). Liang in Shen (1994) sta poročala o tekmovalnem odnosu na ravni privzema v rastline med Si in B, medtem ko Nable in sod. (1990b) tega učinka niso zaznali. Pozitiven učinek Si se navzven kaže v izboljšanju uspevanja rastlin (Gunes in sod. 2007a, Inal in sod. 2009, Soylemezoglu in sod. 2009, Kaya in sod. 2011). Pozitiven učinek Si na rast rastlin so opazili tudi ob nezadostnih koncentracijah B. Ob dodatku Si v tovrstnih razmerah se namreč povišata stopnja fotosintezne aktivnosti ter stopnja privzema B v rastline (Liang in Shen 1994, Hanafy Ahmed in sod. 2008).

Zaščita pred boleznimi in objedanjem

Poleg blaženja negativnih vplivov številnih abiotskih dejavnikov Si rastlinam nudi zaščito tudi v primeru stresnih biotskih dejavnikov, kamor spadajo tako bolezni kot objedanje (Ma in Takahashi 2002, Tripathi in sod. 2017).

Bolezni

Silicij ščiti rastline pred okužbami mnogih večinoma glivnih patogenov (Preglednica 10). Pogosto je mehanizem, s katerim rastline preko Si preprečujejo napade patogenov, povezan s povišanjem razmerja C/N na račun znižanja koncentracije topnega N v rastlinah. Napade patogenov rastline onemogočajo tudi z odlaganjem Si na površini tkiv. Na ta način se ustvari zaščitna plast, ki patogenom neposredno preprečuje fizični prodor (Ma in Takahashi 2002) na račun otrdevanja teh tkiv (Hattori in sod. 2003), ali zavira encimsko razgradnjo in s tem posreden prodor patogenov v njihova tkiva (Ma in Takahashi 2002). Si nudi zaščito pred patogeni tudi preko sprožitve delovanja različnih zaščitnih encimov, kot sta npr. peroksidaza in polifenol oksidaza, povečane tvorbe lignina (Cai in sod. 2008), sprožitve kaskadnih reakcij in povečanega izražanja zaščitnih genov, povečanja koncentracije različnih zaščitnih (predvsem fenolnih) snovi (Chérif in sod. 1994, Fawe in sod. 1998, Bélanger in sod. 2003, Rodrigues in sod. 2003a, 2004, Fauteux in sod. 2005, Rémus-Borel in sod. 2005, Fauteux in sod. 2006, Rémus-Borel in sod. 2009, Song in sod. 2016) ter povišane stopnje fotorespiracije pri napadenih rastlinah, s čimer zaščiti njihov fotosintezni aparat (Van Bockhaven in sod. 2015). Liang in sod. (2005d) so ugotovili, da foliarno dodajanje Si zaščito omogoča le v fizičnem smislu ali na račun osmotskega učinka, medtem ko odziv na molekularni ravni lahko dosežemo z vnosom Si preko korenin. Tudi Guével in sod. (2007) so podobno poročali, da je foliarno dodajanje Si manj učinkovito od vnosa preko korenin. Carver in sod. (1998) so v svoji raziskavi prišli do nekoliko drugačnih zaključkov kot prej omenjene raziskave. Aktivnost encima fenilalanin amonij liaze in s tem koncentracija fenolnih snovi pri okuženih rastlinah je bila večja v odsotnosti Si, kar so utemeljili kot nadomeščanje zaščite pred patogeni, ki jo sicer nudi Si (Carver in sod. 1998). Djamin in Pathak (1967) sta poročala o tem, da je stopnja zaščite pred patogeni sorazmerna s količino Si, ki se razlikuje med različnimi genotipi iste vrste. Veliko kasneje so Deren in sod. (1994) v svoji raziskavi prišli do drugačnega zaključka, in sicer da večja količina Si pri različnih genotipih iste vrste ne pomeni nujno tudi večje stopnje zaščite pred napadi patogenov.

Preglednica 10: Patogeni, katerih napade na naštete rastlinske vrste omejuje silicij (Si). Vrste patogenov, ki se ponovijo pri različnih rastlinskih vrstah, imajo poleg imena dodatno številčno oznako ([1], [2], [3]…).
Table 10: Pathogens, whose attacks on the listed plant species are restricted by silicon (Si). Pathogen species that appear with multiple plant species have an additional numerical sign ([1], [2], [3]…).

Rastlinska vrsta	Patogen	Viri
riž	*Magnaporthe grisea* (T.T. Hebert) M.E. Barr [1]	Datnoff in sod. (1991), Seebold in sod. (2000, 2001), Kim in sod. (2002), Rodrigues in sod. (2003a, 2004), Seebold in sod. (2004), Rodrigues in sod. (2005), Ranganathan in sod. (2006), Cai in sod. (2008), Hayasaka in sod. (2008), Nakata in sod. (2008), Sun in sod. (2010)
	Cochliobolus miyabeanus (S. Ito & Kurib.) Drechsler ex Dastur	Datnoff in sod. (1991), Winslow (1992), Dallagnol in sod. (2014), Van Bockhaven in sod. (2015)
	Rhizoctonia solani J.G. Kühn	Winslow (1992), Deren in sod. (1994), Rodrigues in sod. (2001, (2003b), Schurt in sod. (2014, 2015)
	Chilo suppressalis Walker	Djamin in Pathak (1967)
	Xanthomonas oryzae (ex Ishiyama) Swings et al. emend. van den Mooter and Swings	Song in sod. (2016)
	Sarocladium attenuatum W. Gams & D. Hawksw.	Winslow (1992)
	Cochliobolus lunatus R.R. Nelson & F.A. Haasis	Winslow (1992)
	Monographella albescens (Thüm.) V.O. Parkinson, Sivan. & C. Booth	Winslow (1992), Tatagiba in sod. (2014)
pšenica	*Blumeria graminis* (DC.) Speer [2]	Bélanger in sod. (2003), Rodgers-Gray in Shaw (2004), Rémus-Borel in sod. (2005), Guével in sod. (2007), Rémus-Borel in sod. (2009)
	Phaeosphaeria nodorum (E. Müll.) Hedjar.	Rodgers-Gray in Shaw (2004)
	Mycosphaerella graminicola (Fuckel) J. Schröt.	Rodgers-Gray in Shaw (2004)

Rastlinska vrsta	**Patogen**	**Viri**
	Oculimacula yallundae (Wallwork & Spooner) Crous & W. Gams	Rodgers-Gray in Shaw (2004)
	Magnaporthe grisea [1]	Aucique Perez in sod. (2014), Debona in sod. (2014), Rios in sod. (2014), Antunes da Cruz in sod. (2015a,b), da Silva in sod. (2015a)
oves	*Blumeria graminis* [2]	Carver in sod. (1998)
ječmen	*Blumeria graminis* [2]	Carver in sod. (1987), Wiese in sod. (2005)
proso	*Sclerospora graminicola* (Sacc.) J. Schröt.	Deepak in sod. (2008), Sapre in sod. (2013)
sirek	*Colletotrichum sublineolum* Henn. ex Sacc. & Trotter	Resende in sod. (2013)
bananovec	*Cylindrocladium spathiphylli* Schoult., El-Gholl & Alfieri	Vermeire in sod. (2011)
	Fusarium oxysporum Schltdl.	Fortunato in sod. (2012, 2014)
	Mycosphaerella fijiensis M. Morelet	Kablan in sod. (2012)
oljna palma	*Ganoderma boninense* Pat.	Najihah in sod. (2015)
mormodika	*Pythium aphanidermatum* (Edson) Fitzp. [3]	Heine in sod. (2007)
paradižnik	*Pythium aphanidermatum* [3]	Heine in sod. (2007)
krompir	*Fusarium sulphureum* Schltdl.	Li in sod. (2009)
fižol	*Pseudocercospora griseola* (Sacc.) Crous & U. Braun	Rodrigues in sod. (2010)
	Colletotrichum lindemuthianum (Sacc. & Magnus) Briosi & Cavara	Polanco in sod. (2013), Antunes da Cruz in sod. (2014), Polanco in sod. (2014), Rodrigues in sod. (2015)
grah	*Mycosphaerella pinodes* (Berk. & A. Bloxam) Vestergr.	Dann in Muir (2002)
soja	*Phakopsora pachyrhizi* Syd. & P. Syd.	Arsenault-Labrecque in sod. (2012), Antunes Cruz in sod. (2014b)
	Cercospora sojina Hara	Nascimento in sod. (2014)
kumara	*Pythium aphanidermatum* [3]	Chérif in sod. (1994)
	Pythium ultimum Trow	Chérif in sod. (1992, 1994)
	Cladosporium cucumerinum Ellis & Arthur	Fawe in sod. (1998)
	Sphaerotheca fuliginea (Schltdl.) Pollacci [4]	Adatia in Besford (1986), Menzies in sod. (1991), Samuels in sod. (1991a,b), Menzies in sod. (1992), Fawe in sod. (1998), Liang in sod. (2005d)
melona	*Sphaerotheca fuliginea* [4]	Menzies in sod. (1992)
	Podosphaera xanthii (Castagne) U. Braun & Shishkoff [5]	Dallagnol in sod. (2012)
	Acidovorax citrulli Schaad et al.	Ferreira in sod. (2015)
oljna buča	*Podosphaera xanthii* [5]	Heckman in sod. (2003), Torlon in sod. (2016)
	Erysiphe cichoracearum DC. [6]	Menzies in sod. (1992)
	Sphaerotheca fuliginea [4]	Mohaghegh in sod. (2015)
paprika	*Phytophthora capsici* Leonian	French-Monar in sod. (2010)
vinska trta	*Uncinula necator* (Schwein.) Burrill	Bowen in sod. (1992), Reynolds in sod. (1996)
repnjakovec	*Erysiphe cichoracearum* [6]	Ghanmi in sod. (2004), Fauteux in sod. (2006), Vivancos in sod. (2015)
kavovec	*Hemileia vastatrix* Berk. & Broome	Carré-Missio in sod. (2014)
bombaž	*Colletotrichum gossypii* Southw.	Nogueira de Moura Guerra in sod. (2014)
jagodnjak	*Podosphaera aphanis* (Wallr.) U. Braun & S. Takam.	Kanto in sod. (2006), Fatema (2014)
češnja	*Penicillium expansum* Link	Qin in Tian (2005)
	Monilinia fructicola (G. Winter) Honey	Qin in Tian (2005)
vrtnica	*Diplocarpon rosae* F.A. Wolf	Gillman in sod. (2003)
	Podosphaera pannosa (Wallr.) de Bary	Shetty in sod. (2012)

Objedanje

Z nalaganjem Si v rastlinska tkiva se zmanjša pogostost napadov številnih rastlinojedov iz razreda insektov ter sesalcev (Preglednica 11). Si namreč povečuje stopnjo obrabe obustnega aparata napadalcev, zavira njihove napade na račun zmanjšane tvorbe N spojin (Ma in Takahashi 2002, Massey in Hartley 2006), poveča trdnost tkiv, izražanje zaščitnih genov in stopnjo aktivnosti določenih zaščitnih encimov ter koncentracijo različnih zaščitnih snovi (Gomes in sod. 2005, Ye in sod. 2013, Han in sod. 2016). Côté-Beaulieu in sod. (2009) so v svoji raziskavi raziskali možnost uporabe organskih Si spojin za zaščito pred rastlinojedi in ugotovili, da kljub njihovi večji topnosti in s tem večjim potencialom uporabe Si kislina ostaja edina možna oblika Si, ki lahko služi kot zaščita pred rastlinojedi. Organske Si spojine namreč po določenem času postanejo fitotoksične (Côté-Beaulieu in sod. 2009). Objedanje sproža nalaganje Si v rastlinah, kar se nato zrcali v boljši fizični zaščiti rastlin pred objedanjem (Hartley in DeGabriel 2016). Cooke in Leishman (2012) sta prišli so ugotovitve, da je zaščita s Si pred objedanjem v primeru nekaterih rastlinojedov bolj učinkovita od običajne in energetsko zahtevnejše zaščite rastlin s C spojinami (kot je npr. lignin). Vseeno se izkaže, da najučinkovitejšo zaščitno strategijo predstavlja kombinacija Si in lignina (Piperno 2006), zato pogosto prihaja do kompromisa ter iskanja ravnovesja med koncentracijo Si in zaščitnimi C spojinami (Cooke in Leishman 2012). Podobno kot sta Djamin in Pathak (1967) pokazala glede soodvisnosti med količino Si in stopnjo zaščite pred napadi patogenov, so Katz in sod. (2014) ugotovili, da je tudi stopnja zaščite pred objedanjem nižja pri rastlinah, ki že v osnovi vsebujejo nižje koncentracije Si. Različna zmožnost rastlinskih vrst za privzem in kopičenje Si ob napadih rastlinojedov pomeni različno stopnjo tekmovalne prednosti posameznih vrst. Iz tega sledi, da Si ne igra pomembne vloge le na ravni posameznih osebkov, temveč kroji tudi strukturo rastlinskih združb (Garbuzov in sod. 2011), saj močno vpliva na populacijsko dinamiko rastlinojedih napadalcev (Reynolds in sod. 2012). V raziskavi, ki so jo objavili Doğramaci in sod. (2013), se ob dodatku Si stopnja objedanja na paprikah ni zmanjšala. Kot razlog za to so navedli nezadostno količino nakopičenega Si v tkivih teh rastlin (Doğramaci in sod. 2013). Podobno tudi Lanning (1966) ni ugotovil neposredne povezave med količino Si in zaščito pred boleznimi ali objedanjem. Sanson in sod. (2007) so ob preizkušanju trdote Si fitolitov in sesalske sklenine ugotovili, da je slednja trdnejša in iz tega sklepali, da Si ni glavni razlog za povečano obrabo zob pri sesalcih. Shewmaker in sod. (1989) so pokazali, da količina Si ne narekuje izbire krme pri ovcah. Slednji raziskavi nakazujeta, da Si najverjetneje boljšo zaščito pred rastlinojedi nudi v primeru nevretenčarjev kot v primeru vretenčarjev (Vicari in Bazely 1993). Tudi novejše in bolj evolucijsko obarvane raziskave se nagibajo k dejstvu, da Si nima tako odločilne vloge pri odvračanju objedanja s strani rastlinojedih sesalcev, kot je sprva veljalo (Strömberg 2002, Prasad in sod. 2005, Strömberg in sod. 2016). Strömberg (2002) ter Strömberg in sod. (2016) to domnevo utemeljujejo na podlagi ugotovitev, da je ponekod travnata pokrajina prevladovala že vsaj 7 milijonov let pred domnevnim pojavom prilagoditev zobovja rastlinojedih sesalcev na trave ter da so trave postale akumulatorji Si že 37 milijonov let preden so se ti sploh razvili (Strömberg 2002, Strömberg in sod. 2016), Prasad in sod. (2005) pa na podlagi nizke vsebnosti fitolitov v fosilnih iztrebkih takratnih rastlinojedih sesalcev in posledično ugotovitve, da trave v takratnem obdobju niso predstavljale glavnega vira hrane za to živalsko skupino. Kot glavne krivce za selekcijski pritisk na trave v smislu kopičenja Si so označili rastlinojede žuželke ali le manjše rastlinojede sesalce (Prasad in sod. 2005).

Preglednica 11: Rastlinojedi, katerih napade na naštete rastlinske vrste omejuje silicij (Si). Vrste rastlinojedov, ki se ponovijo pri različnih rastlinskih vrstah, imajo poleg imena dodatno numerično oznako (^{1}, ^{2}, ^{3}…).

Table 11: Herbivores, whose attacks on the listed plant species are restricted by silicon (Si). Herbivore species that appear with multiple plant species have an additional numerical sign (^{1}, ^{2}, ^{3}…).

Rastlinska vrsta	**Rastlinojedi**	**Viri**
riž	*Cnaphalocrocis medinalis* Guenée (Insecta, Lepidoptera)	Ye in sod. (2013), Han in sod. (2016)
	Scirpophaga incertulas Walker (Insecta, Lepidoptera)	Ranganathan in sod. (2006), Jeer in sod. (2016)
	Sogatella furcifera Horvath (Insecta, Hemiptera)	Salim in Saxena (1991)
	Agriolimax reticulatus Müller (Mollusca, Gastropoda)	Wadham in Parry (1981)
	Nilaparvata lugens Stål (Insecta, Hemiptera)	He in sod. (2015)
pšenica	*Schizaphis graminum* Rondani (Insecta, Hemiptera, Aphididae)	Basagli in sod. (2003), Moraes in sod. (2004), Gomes in sod. (2005), Goussain in sod. (2005)
	Oryctolagus cuniculus Linnaeus (Mammalia, Leporidae)	Cotterill in sod. (2007)
koruza	*Ostrinia nubilalis* Hübner (Insecta, Lepidoptera)	Coors (1987)
sladkorni trs	*Eldana saccharina* Walker (Insecta, Lepidoptera)	Kvedaras in sod. (2005, 2007a,b)
	Diatraea saccharalis Fabricius Insecta, Lepidoptera)	Sartori de Camargo in sod. (2014)
stoklasa	*Microtus ochrogaster* Wagner (Mammalia, Cricetidae)	Gali-Muhtasib in sod. (1992)
ljuljka	*Schistocerca gregaria* Forsskål (Insecta, Orthoptera) ^{1}	Massey in sod. (2007), Hunt in sod. (2008), Garbuzov in sod. (2011)
	Microtus agrestis Linnaeus (Mammalia, Cricetidae) ^{2}	Massey in Hartley (2006), Massey in sod. (2007)
	Oscinella frit Linnaeus (Insecta, Diptera)	Moore (1984)
	Spodoptera exempta Walker (Insecta, Lepidoptera) ^{3}	Massey in Hartley (2009)
bilnica	*Schistocerca gregaria* (Insecta, Orthoptera) ^{1}	Massey in sod. (2007), Hunt in sod. (2008)
	Microtus agrestis (Mammalia, Cricetidae) ^{2}	Massey in Hartley (2006), Massey in sod. (2007)
	Spodoptera exempta (Insecta, Lepidoptera) ^{3}	Massey in Hartley (2009)
masnica	*Microtus agrestis* (Mammalia, Cricetidae) ^{2}	Massey in sod. (2008)
	Spodoptera exempta (Insecta, Lepidoptera) ^{3}	Massey in Hartley (2009)
kumara	*Bemisia tabaci* Gennadius (Insecta, Hemiptera)	Correa in sod. (2005)
krizantema	*Macrosiphoniella sanborni* Gillette (Arthropoda, Hemiptera, Aphididae)	Jeong in sod. (2012)
kavovec	*Meloidogyne exigua* Göldi (Nematoda)	da Silva in sod. (2015b)

Raziskave ter uporaba silicija v kmetijstvu

Z raziskovanjem učinkov Si na rastline so se zelo intenzivno ukvarjali na Japonskem. Največ raziskav so izvedli v povezavi z rižem, ki je njihova najpomembnejša poljščina. Riž za svoje uspevanje potrebuje ogromne količine Si, ki si jih po naravni poti pri obstoječem načinu pridelovanja ne more zagotoviti. Tako je leta 1955 Japonska postala prva država na svetu, ki je odobrila gnojenje s Si. Sprva so kot gnojilo uporabljali jalovino iz železarn in jeklarn, ki vsebuje veliko Ca silikata in s tem Si. Zaradi veliko večje vsebnosti Ca kot Si ter pojavljanja drugih kovin v jalovini, ki imajo kljub nižjim koncentracijam lahko večji vpliv na različne fiziološke procese, so sčasoma pričeli razvijati alternativna Si gnojila, kot so običajno Mg fosfatno gnojilo z višjo vsebnostjo Si, K silikat ter silika gel, ki poleg Si ne vsebuje drugih primesi, a je znatno dražji (Ma in Takahashi 2002). Poleg naštetih gnojil kot vir Si za rastline lahko uporabimo tudi naravni volastonit ali diatomejsko zemljo (Heckman 2013), ga dodajamo v obliki nanodelcev nano-SiO_2 (Saxena in sod. 2015), ali pa enostavno vzdržujemo zadostno količino Si v tleh s puščanjem odvečne biomase na pridelovalnih površinah. S tem omogočimo vračanje Si nazaj v tla preko postopnega razgrajevanja rastlinskega materiala (Ma in Takahashi 2002). Si rastlinam lahko dodajamo preko tal ali foliarno (Bowen in sod. 1992, Menzies in sod. 1992). Slednji način je najverjetneje bolj učinkovit za rastline s pasivnim ali izključevalnim načinom privzema Si iz tal (Ma in Takahashi 2002).

Kljub vsesplošnemu pojavljanju Si tako v tleh kot v rastlinah so se raziskovalci z vlogo Si v rastlinah pričeli ukvarjati dokaj pozno (Ma in Takahashi 2002). Poleg že omenjene globoko zakoreninjene stare definicije esencialnosti elementov in s tem nepriznavanja Si kot pomembnega elementa za rast in razvoj rastlin (Epstein 1994, 1999, 2009) bi to neskladnost lahko pojasnili na podlagi njegove velike zastopanosti v tleh, saj iz tega vzroka zelo redko pride do pomanjkanja Si v rastlinah, poleg tega pa simptomi pomanjkanja Si niso tako opazni kot v primeru nekaterih drugih elementov (Ma in Takahashi 2002). Človeška populacija dandanes narašča izredno hitro, sorazmerno s tem pa raste tudi naša potreba po hrani. Posledično vse bolj primanjkuje optimalnih obdelovalnih površin za pridelavo, zaradi česar smo vedno pogosteje rastline prisiljeni gojiti tudi na manj rodovitnih tleh in v bolj stresnih razmerah (Tripathi in sod. 2017). K vedno večji pogostosti pojavljanja različnih motenj in stresnih razmer za rastline ter v povezavi s tem za okolje in zdravje vseh živih bitij obremenjujoče pretirane uporabe umetnih pesticidov in fungicidov še dodatno pripomore naše intenzivno globalno spreminjanje okolja v današnjem času (Ma in Takahashi 2002). Glede na trenutne razmere in obete za prihodnost bo Si s svojimi vsestranskimi koristnimi funkcijami zagotovo postal vse pomembnejši na področju gojenja kmetijskih rastlin (Cooke in sod. 2016b, Tripathi in sod. 2017). Njegov potencial se zrcali predvsem v dejstvu, da 7 od 10 najbolj gojenih poljščin na svetu spada med akumulatorje Si (Guntzer in sod. 2012). Z genetsko modifikacijo izključevalcev Si na ta način, da bi privzemali več Si (Ma in Takahashi 2002, Ma 2004, Ma in Yamaji 2006), bi se njegova uporabnost v kmetijstvu še povečala. En primer tovrstne genetske modifikacije je opisan v raziskavi, ki so jo opravili Sahebi in sod. (2015). Ugotovili so, da so transgene rastline z vstavljenim genom za protein, bogat s serinom, zaradi povečane vsebnosti serina privzemale in kopičile več Si ter s tem pokazali na potencial tega postopka pri povečanju tolerance rastlin do različnih stresnih dejavnikov (Sahebi in sod. 2015). Potrebno pa se je zavedati, da smo skozi stoletja s stalnim odnašanjem pridelka z obdelovalnih površin ponekod že izdatno izčrpali zaloge rastlinam dostopnega Si v tleh, zato bo v prihodnosti za povečanje pridelka določenih kmetijsko pomembnih vrst najverjetneje potrebno tudi dodajanje Si v tla (Haynes 2014).

Prispevkov o Si v povezavi z rastlinami se je do danes nabralo že mnogo, predvsem v zadnjem času, in njihovo število še vedno skokovito narašča. Sorazmerno s tem se krepi tudi naše zavedanje o pomenu Si. O vsem tem priča dejstvo, da od leta 1999 naprej vsaka tri leta poteka mednarodna konferenca na temo Si v kmetijstvu, kjer se zberejo raziskovalci s celega sveta in predstavijo svoje najnovejše izsledke na tem področju. Do sedaj je se je tako zvrstilo že sedem tovrstnih konferenc. Naslednja bo pod okriljem združenja ISSAG (The International Society for Silicon in Agriculture and Related Disciplines) potekala oktobra 2020 v Združenih državah Amerike (ISSAG 2019).

Povzetek

Silicij je drugi najbolj zastopan element v tleh, v rastlinah pa njegov delež sega vse od 0,1 do 10 % njihove suhe mase ali celo več. To kaže, da ni le pomemben gradnik tal, temveč tudi rastlin. Glede na način privzema silicija iz tal rastline uvrščamo v tri tipe, in sicer akumulatorje silicija z aktivnim privzemom in vsebnostjo silicija > 1 %, intermediate s pasivnim privzemom silicija ter izključevalce silicija z vsebnostjo silicija < 0,5 % in zavračanjem njegovega privzema. Privzem silicija v obliki silicijeve kisline iz tal v rastline poteka preko korenin, njegov prenos po sami rastlini pa nadalje poganja transpiracijski tok. Na vsebnost silicija v rastlinah vpliva tudi njegova dostopnost v tleh ter nekateri drugi abiotski in biotski dejavniki. Ko se silicij odloži v tarčnih celicah, njegovo prerazporejanje ni več možno. Nalaga se predvsem v celičnih stenah celic povrhnjice listov v obliki silicijevega dioksida, pri čemer z naraščajočo koncentracijo nastajajo vrstno značilni fitoliti različnih oblik in velikosti.

Razlike v vzorcu nalaganja silicija v rastlinah se kažejo tako na filogenetskem nivoju kot tudi med različnimi funkcionalnimi tipi rastlin. Vsebnost silicija v rastlinskih tkivih se običajno povečuje tekom življenja rastlin. Silicij predstavlja alternativo ogljiku s strukturnega in podpornega vidika, saj za rastline predstavlja 10–20 krat manj potraten vir od ogljika. Sposobnost aktivnega kopičenja silicija v rastlinah se je tekom evolucije razvila večkrat neodvisno, saj akumulatorje silicija najdemo tako med evolucijsko starimi kot tudi mladimi taksoni. Pri travah je ta lastnost močno pridobila na pomenu z upadom koncentracije atmosferskega ogljikovega dioksida v poznem miocenu. Eno od gonilnih sil za večjo stopnjo silicifikacije pri travah bi lahko predstavljal tudi koevolucijski odnos med travami in rastlinojedimi sesalci. Silicij je pomemben za normalno uspevanje vseh rastlin, poleg tega pa jim nudi številne koristi v stresnih okoliščinah preko mnogih različnih mehanizmov. Pripomore k večji fotosintezni aktivnosti, pomaga pri uravnavanju neravnovesja nekaterih pomembnejših hranil, ščiti rastline pred sušo, povišano slanostjo in povečano stopnjo UV sevanja, blaži stres zaradi ekstremnih temperatur in zmanjšuje negativne učinke različnih kovin ter nekaterih drugih elementov. Rastlinam omogoča tudi učinkovito zaščito pred boleznimi in objedanjem. Z vlogo silicija pri rastlinah so se prvi začeli intenzivno ukvarjati Japonci. Izvedli so ogromno raziskav na rižu kot svoji najpomembnejši poljščini, ki za svoje uspevanje zahteva ogromno silicija, in kot prva država na svetu odobrili gnojenje s silicijem. Rastlinam silicij lahko dodajamo preko tal ali foliarno. Ob današnjem skokovitem povečevanju potreb hitro naraščajočega prebivalstva ter s tem tudi vedno večjim obremenjevanjem okolja ustvarjamo vedno manj ugodne razmere za gojenje kmetijskih rastlin. Silicij bo tako s svojimi vsestranskimi koristmi za rastline v stresnih razmerah zagotovo v kmetijstvu postajal vse pomembnejši. Njegov potencial je zelo velik že ob dejstvu, da 7 od 10 najpomembnejših poljščin sveta spada med akumulatorje silicija, z genetsko modifikacijo izključevalcev silicija na ta način, da bi privzemali več silicija, pa bi se njegova uporabnost v kmetijstvu še dodatno povečala.

Summary

Silicon is the second most abundant element in soil, and in plants its proportion ranges from 0.1 to 10% of their dry weight, or even more. This shows that it is not only an important constituent of soil, but also of plants. Depending on the mode of silicon uptake from soil, plants are classified into three types, namely silicon accumulators with active uptake and silicon contents of > 1%, intermediates with passive silicon uptake, and silicon excluders with silicon contents of < 0.5%, which reject its uptake. Silicon is taken up by plants from soil in the form of silicic acid *via* roots, and its transfer along the plant is driven by transpiration flow. The content of silicon in plants is also affected by its availability in the soil and some other abiotic and biotic factors. When silicon is deposited in target cells, its redistribution is no longer possible. It mainly accumulates in cell walls of leaf epidermal cells in the form of silicon dioxide, with increasing silicon contents resulting in formation of species-specific phytoliths of various shapes and sizes. Silicon loading patterns vary not only according to different phylogenetic level, but also between different plant functional types. Silicon content in plant tissues usually increases during plants' lifetime. Being 10–20-fold less expensive as a source for plants, silicon represents an alternative to carbon in terms of structure and support. The ability of plants to actively accumulate silicon evolved many times independently, as silicon accumulators are found both among evolutionary old and young taxons. In grasses, silicon has gained importance with the decrease in atmospheric carbon dioxide concentration in the late Miocene. One of the major driving forces for a greater degree of silicification in grasses could also be the coevolutionary relationship between grasses and herbivorous mammals. Silicon is crucial for normal growth of all plants, and offers many benefits to plants in stressful conditions through numerous different mechanisms. It helps to increase photosynthetic activity and equilibrate the unbalance of some important nutrients, protects plants against drought, increased salinity, and increased UV radiation, ameliorates stress due to extreme temperatures, and mitigates negative effects of various metals and some other elements. It also provides effective

protection against plant diseases and herbivory. Japanese researchers were the first to start dealing intensively with the role of silicon in plants. They carried out enormous research on rice as their most important crop plant, which requires great amounts of silicon for successful growth, and were the first country in the world to approve fertilisation with silicon. Silicon can be applied to plants by soil or foliarly. With today's rapidly growing world population and consequently steeply rising demands of the mankind, we are continuously creating less and less favourable conditions for cultivation of agricultural plants. Silicon will thus become more and more important in agriculture due to its manifold beneficial roles in plants under stressful conditions. Its potential is already very high considering the fact that 7 out of the 10 most important crops of the world are silicon accumulators. However, with genetic modification of silicon excluders in a way that they as well would absorb more silicon, the need for silicon in agriculture would further increase.

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The interactions between UV radiation, drought and selenium in different buckwheat species

Interakcije med UV sevanjem, sušo in selenom pri različnih vrstah ajde

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Abstract: Here we summarise the outcomes on biochemical response and growth of buckwheat with respect to UV radiation, drought and selenium, as well as their interactions. Buckwheats are taxonomically and morphologically very diverse. They have been subjected to more or less intensive breeding, which results in higher susceptibility to environmental constraints including drought and also in different potential to cope and exploit UV radiation. The responses of different buckwheats to UV, drought and their combination differed in different species. Selenium treatment may mitigate negative effects of environmental constraints on buckwheat. Regarding the production of UV absorbing compounds, buckwheats mainly positively respond to UV dose. Ca druses in buckwheat seem to be important in affecting UV penetration.

Keywords: buckwheat, UV radiation, drought, selenium

Izvleček: V prispevku povzemamo biokemijske značilnosti in rast ajde glede na vplive UV sevanja, suše in selena ter njihovih interakcij. Ajda je taksonomsko in morfološko zelo raznolika. Ajda je bila podvržena bolj ali manj intenzivnemu žlahtnjenju, kar ima za posledico večjo dovzetnost za strese zaradi okoljskih omejitev, vključno s sušo in zaščito pred UV sevanjem. Rezultati so pokazali različne odzive različnih vrst ajd na UV sevanje, sušo in njihovo kombinacijo. Količina UV absorbirajočih snovi v ajdi se povečuje z odmerkom UV sevanja. Obravnavanje ajde s selenom lahko omili negativne učinke okoljskih omejitev na ajdo. Pri uravnavanju količine sevanja, ki prodira v tkiva, imajo pomembno vlogo tudi Ca kristali.

Ključne besede: ajda, UV sevanje, suša, selen

Introduction

Different plant species have different abilities to cope with environmental constraints. The success of agricultural crops therefore depends on climate, terrain, soil properties, water availability, and their adaptations to specific environments (Nakabayashi et al. 2014). Agricultural plants are often grown in areas that differ significantly from their domestic environment and have been subjected to intensive breeding in order to increase yield, which in turn may compromise their potential to overcome unfavourable conditions in their environment.

The ozone layer that maintains favourable UV levels at the Earth surface, will presumably recover to the long-term mean that was recorded from 1964-1980 until 2050 (Chipperfield et al. 2015). This is important since enhanced UV radiation significantly affects plant properties and causes stress under elevated levels (Gaberščik et al. 2002). Plants have been subjected to UV radiation during their evolution, and they have evolved mechanisms to fully take advantage of their light environment including UV radiation. Many authors (Prado et al. 2012, Jansen et al. 2012, Björn 2015) even stated that ambient UV radiation presents an evolutionarily-important environmental factor for regulation of plant growth and development, and that ambient UV-B radiation might be more properly viewed as a photomorphogenic signal rather than a stressor for plants under field conditions. In many cases, UV induced plant properties increase the potential of plants to survive under different environmental constraints. UV affects biochemical, morphological, and anatomical plant characteristics, triggers activity of the phenyl-propanoid cycle, causes plant stunting, reductions in leaf area and total biomass, and causes alterations in patterns of biomass partitioning into various plant organs (Rozema et al. 2002). The intensity of UV effects on plants is species-specific and results in potential damage and consequently in activation of protective mechanisms (Gaberščik et al. 2001). Jin et al. (2017) reported about a negative effect of UV-B radiation on both survival and growth in a variety of species differing in their life history, trophic level, and habitat. Ambient UV radiation may cause reduction in biomass, photosynthesis, growth, and yield of many plant species. Nevertheless, these studies suggest that sensitivity to ambient UV radiation varies considerably both within and between plant species (Kataria and Guruprasad 2014). However, the exclusion or reduction of UV radiation during plant growth and development can significantly affect plant traits (Golob et al. 2017a).

Recent Earth′s climate conditions observations indicate that the environmental changes today are faster and greater than in the past. Agricultural productivity all over the world is subjected to increasing environmental constraints, particularly to drought. In recent years, most European countries have been affected by drought (The European Commission 2010, Vanwindekens et al. 2018). This is expected, since among several problems that crop plants face, water stress is the most critical one (Santhosh et al. 2017). A common adverse effect of water stress on crop plants is the reduction in fresh and dry biomass production (Farooq et al. 2009). From 1964 to 2007, national cereal production across the globe had been reduced by 9-10% due to drought and extreme heat (Lesk et al. 2016). In addition, drought and extreme heat are usually related to high radiation environment including UV radiation level. The worsening of the environmental conditions favours the use of crops which are able to survive in harsher environment. Under such conditions some crops can take advantage of high UV radiation, since UV may mitigate the vulnerability of crops to drought (Alexieva et al. 2001, Kakani et al. 2003, Zhang et al. 2011, Germ et al. 2013). Numerous studies revealed that exogenous application of selenium (Se) in small doses to crops increases their tolerance to different environmental conditions (Nawaz et al. 2015, Golob et al. 2017a). Selenium could play a protective role in crops during high UV radiation or water deficit by enhancing the antioxidant enzyme activity (Ekelund and Danilov 2001, Nawaz et al. 2015) and decreasing the content of reactive oxygen species (ROS). Supplemental Se improves growth and yield in wheat and buckwheat subjected to water deficit conditions and increased UV radiation respectively (Nawaz et al. 2015). Despite many positive effects of Se, the physiological mechanisms that underlie those effects have been poorly understood and needs to be elucidated (Hasanuzzaman et al. 2014).

Here we summarise the main research results on interactions between UV radiation, drought and Se in buckwheats. Buckwheat exhibits a lower sensitivity to various types of environmental constraints, due to less intensive breeding, compared to major cereals (Halbrecq et al. 2005). Buckwheat is also attracting attention because it possesses high potential for production of UV-absorbing substances (Kreft et al. 2002, Fabjan et al. 2003). Growing drought-tolerant crops with low nutrient requirement, or at least more resilient crops, is becoming more and more important in today's changing environment with prolonged hot and dry periods. In such manner, we would be able to compensate for the decrease in arable land quality and thus ensure adequate food production for the ever-growing global population in a more sustainable way (Saha et al. 2016, Wang et al. 2016, Kumar et al. 2018). Drought tolerance and resilience of crops depends on a variety of factors like species origin and properties and environmental conditions including UV radiation and mineral nutrition. Special attention in this review will be therefore given to UV, water shortage and the effect of selenium treatment.

Buckwheat is a modest crop

Buckwheat can grow successfully in harsh environment since it has low demands for nutrients and can exhibit high phenotypic plasticity (Li and Zhang 2001, Kreft et al. 2002). In Tibet, it is found at altitudes of up to 4,500 m, therefore it can thrive at high altitudes with elevated UV radiation levels in comparison to lowlands (Bonafaccia et al. 2003). The increase in UV radiation along the altitudinal gradient ranges from between 6% and 8% (Caldwell et al. 1998) to 20% per each 1,000 m of elevation. Buckwheat produces a variety of phenolic compounds, which among others include flavonoids, whose synthesis is significantly enhanced by UV radiation, as shown in many studies (e.g. Gaberščik et al. 2002, Suzuki et al. 2005, Golob et al. 2018a). The most commonly used taxa of buckwheat around the world are common and Tartary buckwheat (Bonafaccia et al. 2003). Tartary buckwheat usually thrives at higher elevations in comparison to common buckwheat (Tsuji and Ohnishi 2001). In searching of possible ancestors of common and Tartary buckwheat it was shown that based on the distribution of their wild ancestors, common buckwheat originates in the northwestern corner of China's Yunnan Province, while Tartary buckwheat originates in the northwest part of Sichuan Province, as also confirmed by the variability of allozymes in the buckwheat (Ohnishi 1998). Wild and cultivated types of Tartary buckwheat exist in the same regions of northeastern Pakistan, Tibet, Yunnan, and Sichuan (Tsuji and Ohnishi 2001, Germ and Gaberščik 2016).

Protection of plants against high UV levels

Buckwheats are C3 plants in which the photosynthetic photon flux density is saturated at about 1000 µmol m^{-2} s^{-1} (Larcher 2003), therefore their efficient protection against excessive radiation is of primary importance, especially if other constraints are present. The fate of the photons that hit the leaf surface depends primarily on the characteristics of the epidermis; namely, epidermal structures, the quantity and quality of phenolic substances (Grašič et al. 2019). Thick epidermal layer with well-developed cuticle is not only the protection against high level of solar radiation, but also presents important protection against water loss. The most important factor affecting the penetration of UV radiation is the production of UV-absorbing compounds like flavonoids and related phenyl-propanoids (Gaberščik et al. 2002). These are regarded as one of the key components of an overall acclimation response of plants to changing UV environments (Barnes et al. 2016). Their production is determined by UV dose, radiation quality, time of exposure and the presence of different environmental constraints including water shortage and the potential of plant species (Ren et al. 2007, Golob et al. 2017a, Golob et al. 2018a). The production of UV absorbing compounds is either inducible (dose dependent) or constitutive (not dose dependent). The latter is mainly characteristic in plants colonising high radiation environments. However, buckwheat mainly shows dose dependent response (Gaberščik et al. 2002). By triggering the secondary metabolic pathway, UV radiation also increases plant antioxidant activity (Sebastian et al. 2018). Indeed, Hideg and Strid (2017) reported that flavonoids have great potential to scavenge reactive oxygen species (ROS), which can be also produced during water shortage. The investigations of Tartary buckwheat showed significant positive correlations between phenolic compounds, the amounts of certain antioxidants and altitude of growing sites (Kishore et al. 2010). In comparison to other taxa, buckwheat exhibits high potential of production of UV-absorbing compounds. One of the most important and researched flavonoids in buckwheat is rutin (Fabjan et al. 2003, Kreft et al. 2006). Suzuki et al. (2015) reported that in buckwheat leaves, rutin and rutin-oxidase are involved in enhancing the defence against UV radiation, low temperature, and desiccation. Regvar et al. (2012) studied the effects of elevated UV-B radiation on concentrations of rutin, catechin, and quercetin in both common and Tartary buckwheat, showing that in common buckwheat, they were induced by UV-B, while there were no differences in the concentrations in the Tartary buckwheat even though the latter contained more total flavonoids. Yao et al. (2006) who studied Tartary buckwheat grown under different UV-B levels showed that UV-B absorbing compounds and rutin concentrations increased under near ambient, but not under elevated UV-B. This may be related to the overall costs needed to prevent UV-B stress at highest radiation level (Suchar and Robberecht 2016). Suzuki et al. (2005) reported that Tartary buckwheat treated with UV light for 30 min showed increased rutin concentration by 122%. This potential is not only leaf specific since UV-B treatment of hairy roots of Tartary buckwheat seedlings also increased rutin and quercetin levels (Huang et al. 2016).

Jovanović et al. (2006) studied the mode of the enzymatic antioxidant defence system in common buckwheat leaves and seedlings subjected to short-term enhanced UV-B radiation showing a considerable increase in methanol-soluble flavonoids, which is in agreement with previously reported data (Gaberščik et al. 2002, Suzuki et al. 2005).

Plant biochemical protection can be also improved by improving plant nutrition. One of important elements benefiting plants is also Se (Golob et al. 2017a). The accumulation of secondary substances can be altered by biotic interactions. The effects of increased UV-B radiation on arbuscular mycorrhiza and secondary metabolite production in common and Tartary buckwheat revealed that root colonisation with arbuscular mycorrhizal fungi significantly reduced catechin concentrations in common buckwheat roots, and induced rutin concentrations in Tartary buckwheat (Regvar et al. 2012). Additional protection against UV-radiation in plants is the presence of calcium oxalate (CaOx) crystals (druses) in the leaf tissue that may contribute to uniform distribution of light within leaves (Kuo-Huang et al. 2007, Gal et al. 2012, Golob et al. 2018b). Their position varies with light intensity and at high intensity, crystals are mainly formed at the top of the palisade cells (He et al. 2014). CaOx druses also reduce the transmission of UV-B through leaves as it was shown in the experiment with Tartary buckwheat where the density of CaOx druses positively correlated with the reflectance in the blue, green, yellow and UV-B regions of the spectrum (Golob et al. 2018b).

Adaptation to drought stress can increase tolerance to UV-B radiation

Vulnerability of crops to UV is affected by different environmental factors namely water regime, ambient levels of visible radiation, and nutrient status (Shen et al. 2015). Elevated UV radiation levels and drought usually occur at the same time under conditions of high solar irradiance and low precipitation rate, which are becoming more and more frequent and extreme (Comont et al. 2012). Clarification of the interaction between drought and UV-B will help us to understand their potential impact on plant adaptation to the changing environmental conditions that will enable efficient crop production (Alexieva et al. 2001, Rodríguez-Calzada et al. 2019). There is an evidence of both synergistic and antagonistic interactions between enhanced UV radiation and drought (Kakani et al. 2003).

Different studies showed that adaptation to drought stress contributes to increased tolerance to UV-B radiation (Hofmann et al. 2003). This is the consequence of specific morphological responses, like thicker cuticle, smaller leaves shorter internodes that are the same for both constraints (Larcher 2003, Jansen et al. 2012). During drought, some plants also enhance the synthesis of phenolic substances and waxes, which improves UV-B radiation screening and reflection and reduces UV-B damaging effects (Kulandaivelu et al. 1997). Alexieva et al. (2001) reported that drought induced activity of antioxidative enzymes that protect plants against oxidative damages caused by UV-B radiation. They also presumed that proline is the drought-induced substance, which plays an important protective role in response to UV-B. However, Caldwell et al. (1998) concluded that drought may cover up UV-B impacts on plants, since drought is a stronger plant stressor than elevated UV-B radiation. However, there are also some opposite findings. Tian and Lei (2007) reported that simultaneous exposure to drought and UV-B caused even stronger damage to wheat seedlings than when these two stress factors were applied separately. This is possibly related to combine oxidative damage. Similarly, the earlier study of Runeckles and Krupa (1994) showed that enhanced UV-B radiation lowered tolerance of crops to drought. Common buckwheat and Tartary buckwheat exposed to different levels of UV-B radiation simulating 17% ozone depletion and water shortage, revealed significant negative effect of elevated UV-B on growth parameters in well-watered common buckwheat, that was less pronounced in drought affected group (Germ et al. 2013). In line with expectations, Tartary buckwheat showed less sensitivity to both stressors, presumably because it had been subjected to breeding to a lesser extent. Enhanced UV-B also significantly reduced total biomass accumulation and biomass allocation to root in well-watered *Fagopyrum dibotrys* plants, while UV-B mitigated the effect of water shortage on biomass accumulation (Zhang et al. 2011). Similarly, Alexieva et al. (2001) found out that UV-B and drought acted synergistically in pea and wheat, inducing protective mechanisms in a way that preapplication of either of the two stress factors lowered the damage, caused by subsequent exposure of plants to the other stressor. Authors evidenced that UV-B exerted a stronger negative effect than drought on the growth of seedlings in both species (Alexieva et al. 2001).

Ameliorative effects of the Se addition on UV-B and drought treatments

Selenium (Se) is regarded as a beneficial nutrient that can increase plant tolerance to different environmental constraints (Yao et al. 2013, Golob et al. 2017a). Ekelund and Danilov (2001) reported that plants, treated with Se, show enhanced tolerance to increased UV-B radiation, due to an antioxidative role of selenium that lowers oxidative damage in plants. It was indicated that addition of Se diminishes the negative influence induced by UV radiation and desiccation (Sieprawska et al. 2015). The addition of Se in appropriate doses can regulate oxidative stress via activation of antioxidative enzymes (Hartikainen et al. 2000) and/or by direct quenching of $O_2\cdot-$ and $OH\cdot$radicals. Se also upregulates the phenyl-propanoid biosynthetic pathway, which results in the accumulation of specific metabolites (Mimmo et al. 2017), such as flavonoids, which have UV absorbing as well as antioxsidant role in plants.

The combined effects of UV-B irradiation and foliar treatment of common buckwheat and Tartary buckwheat with selenium 1 g Se m^{-3} showed that Se treatment mitigated the negative effect of UV-B radiation on plant height and on biomass production in common buckwheat and the effective quantum yield of photosystem II (PS II) in both buckwheat species (Breznik et al. 2005a). Se possibly promotes growth of UV-stressed plants, due to protection of chloroplast enzymes (Breznik et al. 2009). The interaction between Se addition and UV-B radiation in common buckwheat revealed the ameliorative effect of Se for the aboveground biomass, number of nodes, and number of seeds (Breznik et al. 2005b). Smrkolj et al. (2006) treated common buckwheat (*Fagopyrum esculentum* Moench cv. Darja) and Tartary buckwheat (*Fagopyrum tataricum* Gaertn.) by spraying the leaves with Se solution, and exposed the plants to three levels of UV-B radiation. Selenium concentrations in flowers were higher under enhanced UV-B radiation compared to ambient and reduced UV-B radiation conditions in both species. This is in line with study from Ožbolt et al. (2008), where UV-B radiation increased Se content in common buckwheat plants, grown from seeds that were previously soaked in solutions with different Se concentrations.

Golob et al. (2018a) exposed hybrid buckwheat (*F. hybridum*) plants, grown under full and reduced ambient UV radiation to foliar Se treatment. Plants treated with 10 mg L^{-1} sodium selenate contained 20-fold more Se compared to Se-untreated plants, and ambient UV radiation partly reduced this response.

Golob et al. (2007b) studied the impact of Se addition and UV radiation on Tartary and hybrid buckwheat in an outdoor experiment. Tartary buckwheat had higher contents of anthocyanins, UV-B, and UV-A-absorbing substances compared to hybrid buckwheat. Higher contents of protective substances are possibly a consequence of adaptation to unfavourable environmental conditions, as

Tartary buckwheat originates from cooler areas at higher altitudes, often >1,500 m above the sea level.

Se mitigated negative effects of UV-B radiation in common and Tartary buckwheat, but not in hybrid buckwheat. Ameliorative effects of Se in UV-B treated plants were expected, since UV-B radiation causes the production of free radicals. Se upregulates the phenyl-propanoid biosynthetic pathway, which results in the accumulation of specific metabolites.

Summary

Agricultural plants are often subjected to environmental conditions that differ from their home environment so they have to overcome different environmental constrains. Increased UV radiation and drought are commonly present at the same time. The outcomes about joint action of increased UV radiation and drought in buckwheat are diverse. There are evidences of both synergistic and antagonistic interactions. Adaptation to drought stress contributes to increased tolerance to UV-B radiation, which is consequence of specific morphological, biochemical and physiological responses of buckwheat. The responses of buckwheats are different in different species, the UV dose and sites of origin of different cultivars. Some studies have shown that Tartary buckwheat is more tolerant to UV radiation compared to common buckwheat, while the others have shown the same sensitivity. The interactions of UV radiation with drought have also been demonstrated. In the experiments with *F. tataricum* and *F. dibotrys*, UV-B radiation mitigated negative effects of drought, however in *F. esculetum* the effect was less pronounced.

Se mitigated negative effects of UV-B radiation in common and Tartary buckwheat, but not in hybrid buckwheat. Se upregulates the phenyl-propanoid biosynthetic pathway, which results in the accumulation of specific metabolites. All these findings indicate that mineral nutrition of plants is of great importance for plant's protection against increased UV radiation and drought.

Biomineral Ca plays an important role in the genus *Fagopyrum*. CaOx druses in the leaf tissue of the buckwheat interact with the incoming UV light and affect optical properties of the leaves.

Povzetek

Kmetijske rastline so pogosto podvržene okoljskim razmeram, ki se razlikujejo od razmer v njihovem domačem okolju, zato morajo premagati različne okoljske omejitve. Rastline so mnogokrat izpostavljene povečanemu UV sevanju in suši hkrati. Izsledki o vplivih skupnega delovanja UV sevanja in suše so različni. Obstajajo dokazi o sinergističnih in antagonističnih interakcijah. Raziskave so pokazale, da prilagajanje na sušni stres prispeva k večji toleranci na UV-B sevanje, ki je posledica specifičnih morfoloških, biokemijskih in fizioloških odzivov rastlin. Odzivi ajde so različni pri različnih vrstah, odmerkih sevanja in krajih izvora različnih kultivarjev. Nekatere študije so pokazale, da je tatarska ajda bolj tolerantna na UV sevanje v primerjavi z navadno ajdo, druge pa so pokazale njeno precejšnjo občutljivost. Dokazane so bile tudi interakcije UV sevanja s sušo. Pri vrstah *F. tataricum* in *F. dibotrys* je UV-B sevanje omililo negativne učinke pomanjkanja vode, pri vrsti *F. esculetum* pa je bil omilitveni učinek manj izražen.

Se je ublažil negativne učinke UV-B sevanja pri navadni in tatarski ajdi, ni pa imel pozitvnih učinkov pri hibridni ajdi. Se lahko deluje kot antioksidant in niža raven prostih radikalov ter uravnava potek fenilno propanoidnega cikla, kar omogoča kopičenje specifičnih presnovnih produktov. Rezultati kažejo, da je mineralna prehrana rastlin zelo pomembna za varstvo rastlin pred povečanim UV sevanjem in sušo. Pri rodu *Fagopyrum* ima pomembno vlogo tudi biomineral Ca. CaOx kristali v listnem tkivu vplivajo na prehajanje UV svetlobe in na optične lastnosti listov.

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The impact of mowing on the growth and blooming of common ragweed (*Ambrosia artemisiifolia*)

Vpliv košnje na rast in cvetenje pelinolistne žvrklje (*Ambrosia artemisiifolia*)

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Abstract: Common ragweed (*Ambrosia artemisiifolia*) is an invasive alien species originating in North America that has spread widely in Europe in last decades. Removal of common ragweed and prevention of its reproduction is mandatory for landowners in Slovenia, decreed by Slovenian legislation. One of the most commonly used removal methods is mowing, so we decided to conduct a research project on the impact of mowing on the growth and propagation of this species. We used the common ragweed plants that we collected in the spring at the road embankments and planted them in plastic box planters. At the beginning of the summer, we cut the plants at three different heights, which represented a mowing at three different heights. A group of plants was left untreated and represented a control group to compare with the test plants. We monitored their growth until the end of September by measuring the height of plants, the development of male inflorescences, where allergenic pollen is produced, and seed development. We found out that the survival rate of the plants cut above the first pair of leaves were affected the most, while all the plants cut above the third pair and plants of the control group, survived. Plants of control group reached largest height and produced the highest dry mass as well. Contrary to expectations, differences in height and mass of test plants were negligible. Mowing has a major impact on the development of male inflorescences. Mowing above the 1st and 2nd pairs of leaves has reduced the overall length of male inflorescences to a third, while mowing above the 3rd pair almost halved the length of inflorescences. That resulted to a significant reduction in the amount of allergenic pollen. Altogether, most of the fruits (achenes) have grown on control plants. If we calculate the average number of fruits per plant, on average most fruits have developed on control plants and plants cut the lowest. We may conclude that a single mowing in a season does not reduce the production of seeds, which is an important information for maintainers of public areas as well as landowners.

Keywords: *Ambrosia artemisiifolia*, common ragweed, mowing, sexual reproduction

Izvleček: Pelinolistna žvrklja ali pelinolistna ambrozija (*Ambrosia artemisiifolia* L.) je v Evropi zelo razširjena tujerodna vrsta, ki izvira iz Severne Amerike. V Sloveniji nas k njenemu odstranjevanju zavezuje zakonodaja, ki lastnikom zemljišč zapoveduje odstranjevanje ambrozije in preprečevanje njenega razmnoževanja. Eden od najbolj uporabljanih načinov odstranjevanja je košnja, zato smo se odločili izdelati raziskavo o vplivu košnje na rast in razmnoževanje ambrozije. V poskusu smo uporabili rastline, ki smo jih spomladi nabrali ob cesti in jih posadili v cvetlična korita. Rastline smo na začetku poletja porezali na treh različnih višinah (nad 1., 2. in 3. parom listov), kar je predstavljalo košnjo na treh različnih višinah, z namenom opredeliti najprimernejšo višino košnje za učinkovito zatiranje ambrozije. Del rastlin smo pustili neporezanih in so predstavljale kontrolno skupino, s katero smo primerjali testne rastline. Do konca septembra smo spremljali njihovo rast, tako da smo merili višino rastlin, razvoj moških socvetij in razvoj semen. Ugotovili smo, da je propadlo največ rastlin, ki so bile porezane nad prvim parom listov, vse rastline, porezane nad tretjim parom pa so, prav tako kot kontrolne, preživele. Najvišje so zrasle kontrolne rastline, ki smo jim na koncu poskusa izmerili tudi največjo suho maso. V nasprotju s pričakovanji so bile razlike v višinah in masi testnih rastlin zanemarljivo majhne. Velik vpliv ima košnja na razvoj moških socvetij. Košnja nad 1. in 2. parom listov je skupno dolžino moških socvetij zmanjšala na tretjino, košnja nad 3. parom pa skoraj na polovico. To pomeni veliko zmanjšanje količine alergenega peloda. Skupno največ plodov se je razvilo na nepokošenih rastlinah. Če izračunamo povprečno število plodov na rastlino, se je v povprečju največ plodov razvilo na kontrolnih in najnižje pokošenih rastlinah. Enkratna košnja torej ne zmanjša tvorbe semen, kar je pomemben podatek za vzdrževalce javnih površin in lastnike zemljišč.

Ključne besede: *Ambrosia artemisiifolia*, pelinolistna žvrklja, ambrozija, košnja, spolno razmnoževanje

Introduction

Common ragweed (*Ambrosia artemisiifolia* L.) is an invasive alien species originating in North America. Genetic analysis of microsatellite markers in French populations have shown that it was introduced to Europe several times independently (Genton et al. 2005). First records for its presence in Europe are from the middle of 19th Century (Chauvel et al. 2006, Csontos et al. 2010), but its invasive spreading began a few decades ago. In Austria, the first naturalized population was recorded nearly 70 years after the first record of a casual population (Essl et al. 2009). The successful invasion is the result of high seed productivity (Fumanal et al. 2007), seed longevity (Darlington 1922) and effective spreading by the human assisted vectors, as transport of contaminated crops and bird seeds, dirty agricultural and mowing machines and transport of soil (Essl et al. 2009). Common ragweed is the most frequent in Eastern and Central Europe (Buttenschøn et al. 2008–09). First findings in Slovenia are from the middle of 20th Century (Jogan and Vreš 1998). In Europe, the first records were associated with railways (Essl et al. 2009), but later it became frequent also on ruderal sites, fields and bird-feeding sites (Buttenschøn et al. 2008–09, Essl et al. 2009, Strgulc Krajšek and Batič 2014).

Common ragweed is air pollinated annual plant, flowering in late summer. Due to strongly allergenic pollen it has very negative effects on human health (Kofol Seliger 2001). If the population is dense, it also has negative impact on crop yields, especially maize, sugar beet and sunflowers (Buttenschøn et al. 2008–09).

The spread of *Ambrosia* in Slovenia is controlled by two legal instruments. The first is Commission Regulation (EU) No 574/2011 of 16 June 2011, concerned with undesirable contents of animal feed, including *Ambrosia* seeds (Anon. 2011). The second is the Slovene regulation "*Odredba o ukrepih za zatiranje* škodljivih *rastlin iz rodu Ambrosia*" (Decree on measures to suppress harmful plants of genus *Ambrosia*), that obliges every citizen to remove all *Ambrosia* plants from his property to prevent the plants from developing flowers and fruits (Anon. 2010).

The most effective method for the prevention of flowering and reproducing of common ragweed is uprooting the whole plants before the flowering period. When the populations are large, this method is time consuming and too expensive, therefore the most commonly used removal method is mowing (Buttenschøn et al. 2008–09). Common ragweed has well documented regenerative capability and several experiments shown that cutting exclusively cannot control common ragweed (Karrer 2016).

We decided to research the impact of single mowing at three different heights, conducted before the flowering period, on the biomass production, flowering and seed development of *Ambrosia artemisiifolia*, with the aim to prepare a recommendation for the most appropriate cutting height.

Material and methods

We collected the samples of *Ambrosia artemisiifolia* on 16th of June 2017 in Gunclje, in Central Slovenia, in NW suburbs of Ljubljana. Information about the locality: Slovenia: Ljubljana, Gunclje, next to the road between Gunclje and Dvor, lane of grass between the road and pavement, 46° 6’ 13,26” N, 14° 26’ 41,89” E. Leg: Z. Krajšek, Š. Jakoš and S. Strgulc Krajšek, 16th of June 2017.

We gathered about 250 entire young plants, which were 3 to 10 cm tall. Until the planting we stored them in plastic containers. We planted them into elongated plastic box planters (size: 50 × 15 cm), half-filled with mixture of soil (Bio Plantella start, manufacturer Unichem, Vrhnika) and vermiculite in a proportion 2:1, on the same day. In each of 8 box planters we planted 25 ragweed plants. We planted all the remaining plants in the 9th box planter and were planned to be used as source of plants in case of some ragweed plants fail to survive until cutting. We put them on a shady outdoor place without roof so plants were exposed to the local weather. The soil in each box planter have been watered with 1 L of tap water. During the experiment we watered the plants regularly when we saw the soil was getting drier.

On 9th of July 2017 we measured the height of plants and counted pairs of leaves for the first time. Height of each plant has been measured from the soil level to the apical meristem and we counted those fully-developed pairs of leaves, where leaves have been already apart and positioned horizontally. Based on these measurements (Fig. 1) we divided the box planters in 4 groups, containing more or less similar size range and leaf development of plants and decided which box planters will be used for control and which for each experiment treatment:

- plants (N=48) in box planters number 1 and 2 were cut above the first pair of leaves (approx. 1.5–3 cm above the ground),
- plants (N=49) in box planters number 3 and 5 were cut above the second pair of leaves (approx. 2.5–5 cm above the ground),
- plants (N=50) in box planters number 6 and 7 were cut above the third pair of leaves (approx. 4–8 cm above the ground) and
- plants (N=50) in box planters number 4 and 8 were left untreated and were meant for the control group.

We have compared the distribution of plant sizes among all pairs of groups using Tukey‘s Multiple Comparison Test and the differences were never statistically significant. When measuring, we discovered that three plants died. We decided that we would not substitute them with new ones from reserve as the samples were still big enough. We began our experiment on 10th of July 2017. We left box planters on the same place as before.

About month and a half after the beginning of the experiment (on 23rd of August 2017) we measured height of all plants and counted the plants that have developed shoots with male flowers.

The number of living plants included in the experiment was counted twice, 45 days after cutting, and at the end of the experiment, 76 days after cutting.

The experiment has been finished a month later (on 23rd of September 2017). On that day we cut shoots (above ground part of the plant) of each plant just above the soil level and marked them with unique numbers. We (1) put each shoot on white paper and took a photograph, (2) measured

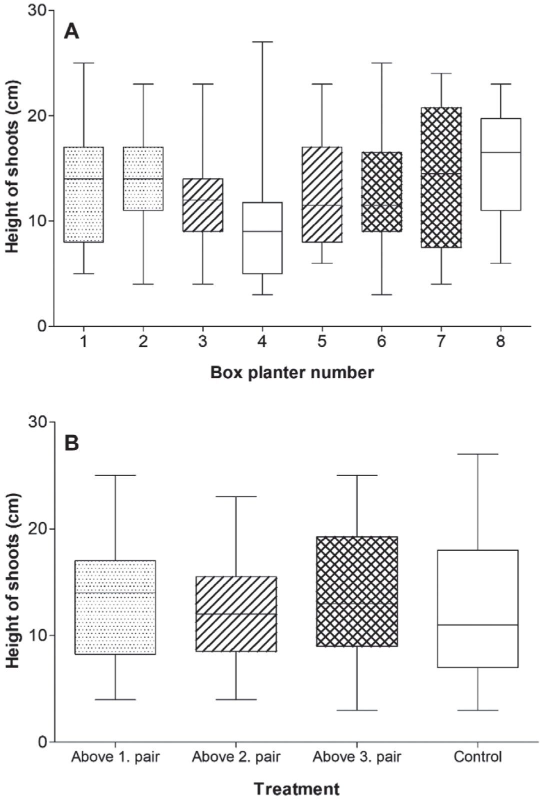

Figure 1: Prior the experiment, the height of shoots was measured in all 8 box planters (A). The box planters were combined in pairs, so the starting intervals of plants' heights before the experiment were similar (no significant difference using Tukey's Multiple Comparison Test) in all four treatments (B).

Slika 1: Pred začetkom poskusa smo izmerili višine rastlin v vseh 8 cvetličnih koritih (A). Korita smo razporedili v pare, tako da smo dobili 4 skupine, ki so imele pred začetkom poskusa čimbolj enak razpored višin rastlin (Tukeyev primerjalni test ni pokazal statistično značilnih razlik, B).

each shoot from the bottom of the stem to the top of the longest shoot, (3) counted the number of branches with male inflorescences on each plant and measured their lengths, and (4) inserted each plant in separate newspaper sheet and let them dry in dryer for herbarium plants.

After drying we weighted each dry plant, collected all seeds from each of them separately and counted them. Plants without seeds have been thrown on compost. Later we combined all seeds that had developed on plants from the same plastic box planters and weighted them together.

On five plant samples we have counted the number of male capitula on 5 cm of the male raceme to calculate the approximate average number of capitula on 1 cm of the male raceme.

Data analyses were carried out in programs MS Excel and GraphPad Prism (Version 5.01, GraphPadPrism Software Inc. 1992–2007).

Results

The number of living plants and the survival rate of plants in different treatments is shown in Tab. 1. All the plants that failed to survive the cutting died in the period of the first 6 weeks after cutting. The lowest survival rate (69%) was

Table 1: Survival rate of *Ambrosia artemisiifolia* in four different experiment groups.
Preglednica 1: Delež preživelih rastlin pelinolistne žvrklje v 4 različnih eksperimentalnih skupinah.

Treatment	Number of plants Cutting 9. 7. 2017	 45th day 23. 8. 2017	 76th day 23. 9. 2018	Survival rate [%]
Control	50	50	50	100
Cut above 1st pair	48	33	33	69
Cut above 2nd pair	49	48	48	98
Cut above 3rd pair	50	50	50	100

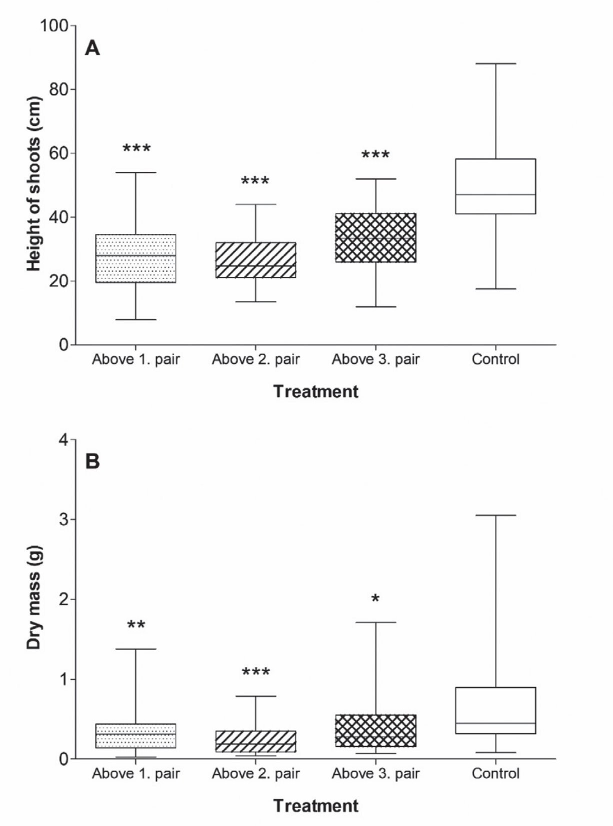

Figure 2: The average height of cut plants at the end of the experiment is significantly shorter than in the control group (Tukey's Multiple Comparison Test), regardless of the height of the cut (A). The average dry mass of aboveground parts of all cut plants was also significantly smaller than in the control group (Kruskal-Wallis Test and Dunn's Multiple Comparison Test, B).

Slika 2: Povprečne višine rastlin v vseh treh skupinah s porezanimi rastlinami so ob koncu eksperimenta statistično značilno nižje od rastlin v kontrolni skupini (Tukeyev primerjalni test, A). Prav tako je statistično značilno manjša suha masa njihovih nadzemnih delov (Kruskal-Wallisov test in Dunnov primerjalni test, B).

observed in group, where plants were cut just above the 1st pair of leaves, in group where plants were cut above the 2nd pair, only 1 plant died, so the survival rate was 98%. In group where plants were cut above the 3rd pair of leaves and in control group all plants survived to the end of experiment.

The plant height and dry mass of aboveground parts of plants were measured at the end of experiment. The average heights of plants that were cut were significantly shorter than in the control group, regardless of the height of the cut (Fig. 2A). The plant heights were measured also in the middle of the experiment (on 45th day). Measured heights were almost the same as at the end of experiment, so plants nearly reached their final height already in August. The dry mass of aboveground parts in all three treatments at the end of experiment was significantly smaller than in the control group (Fig. 2B).

One month before the end of the experiment, all plants from the control group already developed male inflorescences. In the experimental groups, the number of flowering plants was lower (cut above 1st pair of leaves: 76%, cut above 2nd pair of leaves: 91% and cut above 3rd pair of leaves: 94%). Almost all the plants that have been cut developed 2 side shoots with male inflorescence. In the control group, most of the plants had only 1 or 3–4 shoots with male inflorescences. This is connected with plant morphology, as ragweed has opposite leaf arrangement and opposite axillary buds.

The average lengths of male inflorescences at the end of the experiment in all groups are significantly shorter than in the control group, regardless of the height of the cut (Fig. 3A). This confirms that, the cutting decreased the pollen production. The average total length of male inflorescences in the control group was 24 cm. The biggest decrease in the total length of male inflorescences (65% less than in the control group) was observed in the group where plants that were cut above the 2nd pair. The only significant difference between pairs of experiment groups was detected between the group cut above 2nd and 3rd pair, where the plants cut above 2nd pair developed less male inflorescences.

Cutting has almost no influence on the seed (fruit) production. Only the treatment, where plants have been cut above the 2nd pair of leaves, developed significantly less seeds per plant. Cutting above the 1st pair of leaves resulted in production of more seeds as cutting higher on the stem (Fig. 3B). We have also noticed big differences within all 4 groups. Some plants had only a few seeds while the others had more than 100 seeds (Fig. 3B). We have weighted seeds and calculated the average mass of 100 seeds in test groups. In all the test groups the seeds were similar in size. The biggest seeds were produced in the control group but the differences in the mass were not significant.

Discussion

Cutting of *Ambrosia artemisiifolia* plants in the beginning of summer, before the flowering period could reduce the number of surviving plants, but only, when plants were cut very low, above the 1st pair of leaves. In this group 69% survival rate was observed. If plants were cut above 2nd or 3rd pair of leaves, no significant decrease in survival rate was observed. Basset and Crompton (1975) reported that common ragweed in Canada could survive mowing, cutting and trampling. The survival rate of plants cut at 5 cm above ground was 83%. In research conducted in Poland, where tested plants were cut above cotyledons node, the survival rate was 50%, and all plants survived the cutting on higher levels (Tokarska-Guzik et al. 2011).

Growth of *A. artemisiifolia* in early season is slow, internodes are short. In June, rapid upright growth with elongation of younger internodes and growth of shoot in apical meristem starts (Karner 2016). The same author reports, that the growth in height stops in the middle of September, which is different than the results of our experiment, where plants stopped to gain height already in August. In our experiment the average heights and dry mass of aboveground parts of cut plants were significantly lower than in the control group, but the differences among cut groups were not significant. Simard and Benoit (2011) got no significant differences in biomass between mown and intact plants regardless of the mowing time. Plants of *A. artemisiifolia* are very capable to regenerate after cutting, so cutting cannot control growing of common ragweed (Karner 2016).

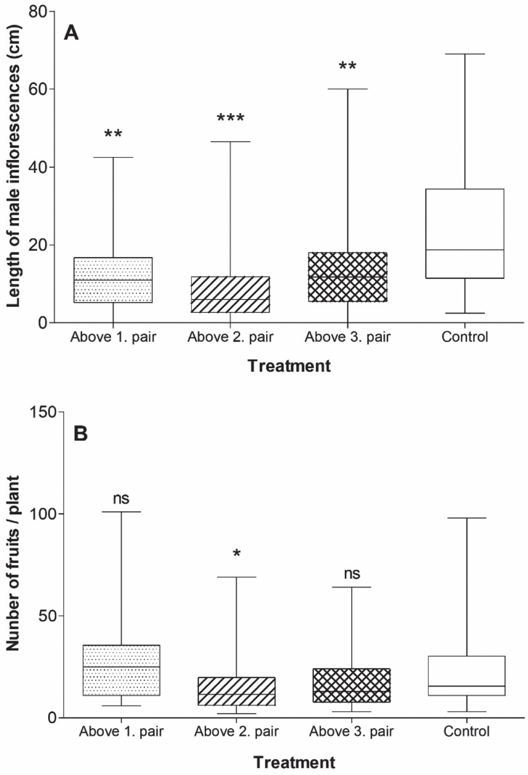

Figure 3: The total lengths of male inflorescences of 2nd order per plant at the end of the experiment in all groups are significantly shorter in comparison with in the control group (Kruskal-Wallis Test and Dunn's Multiple Comparison Test), regardless of the height of the cut (A). Cutting has almost no influence on the seed (fruit) production. The only treatment with significantly less seeds per plant was cut above the 2nd pair of leaves. Cutting above the 1st pair of leaves resulted in production of more seeds than cutting higher on the stem (Kruskal-Wallis Test and Dunn's Multiple Comparison Test, B).

Slika 3: Končna dolžina vseh moških socvetij 2. reda na koncu eksperimenta je bila pri vseh skupinah statistično značilno manjša kot pri kontrolni skupini (Kruskal-Wallisov test in Dunnov primerjalni test, A). Količina semen (plodov) se zaradi rezanja poganjkov ni bistveno zmanjšala. Statistično značilno manjšo količino semen smo prešteli le pri skupini, ki je bila porezana nad 2. parom listov. Rastline, ki so bile porezane nad 1. parom listov, so imele statistično značilno več semen, kot višje porezane rastline (Kruskal-Wallisov test in Dunnov primerjalni test, B).

In the end of August all control plants started to bloom. They developed male inflorescences on primary shoot at least. Over 90% plants that were cut above 2nd and 3rd pair also developed male inflorescences. Only the plants cut above 1st pair had significantly reduced percentage (76%) of plants with male inflorescences. Basset and Crompton (1975) report that common ragweed plants that were cut in July, developed several new stems and started to flower only 10 days later than adjacent uncut plants. Plants cut above cotyledons failed to produce buds of male inflorescences until 2 weeks after cutting (Tokarska-Guzik et al. 2011), but if they were cut higher the percentages of flowering plants were high (over 60%) (Tokarska-Guzik et al. 2011, Simard and Benoit 2011).

Karner (2016) reports that cutting in the time of the beginning of male flowering reduces in 8 times shorter male inflorescences. Simard and Benoit (2011) found out that plants cut twice 10 cm from the ground produced 89% less pollen than intact plants, as cut plants produced less pollen per unit inflorescence length. The same authors report that the average number of pollen grains per intact plant was approximately 4 × 10^8. Only 10 pollen grains per m^3 of air is enough for allergic reaction of the most sensitive people (Buttenschøn et al. 2008–09). It was estimated that 10–30% of Europeans are sensitive to ragweed's pollen (Kofol Seliger 2001). The reduction of pollen production is important, but millions of pollen grains are produced on mowed plant as well.

For the persistence of *A. artemisiifolia* populations and it's spreading, the production of viable seeds is essential. The total number of fruits developed on control plants was the highest in comparison to cut pants, so cutting reduces the amount of seeds. In the experiment conducted by Simard and Benoit (2011) cut plants developed 3–4 times less seeds than control plants. They have cut the plants twice. If the cutting is done only once, the timing is very important (Karner 2016). The best results with almost no vital seeds were achieved if the cutting was carried out in beginning of September (Bohren et al. 2005), but this mowing time is too late if we want to reduce the pollen production. We have calculated the number of seeds per plant in all test groups. The result, that the plants that were cut above 1st pair of leaves produced the highest amount of seeds, was surprising as all published results show the reduction of seed production in cut plants (Bohren et al. 2005, Simard and Benoit 2011, Karner 2016). The average number of seeds per plant was even higher than in the control group, but the difference was not significant. Results of some published experiments show, that mowing reduces not only the number, but also the viability of seeds (Bohren et al. 2005, Simard and Benoit 2011).

For the control of common ragweed, hand pulling before the flowering is still the most effective method. Mowing could reduce the number of surviving plants and the total amount of pollen and seeds, but absolutely not enough. Single mowing is ineffective. Due to very high reproduction capacity of common ragweed plants (Karner 2016) and longevity of viable seeds that could germinate even after 40 years (Darlington 1922), the control of the species remains a challenge for landowners to fulfil the obligation prescribed under the Slovene legislation (Anon 2011). As the most effective method is removal of whole plants before flowering, it is very important to educate people to recognize the plant in early stage of development. Common ragweed is not growing only along roads, on abandoned land and on fields, but it could appear e. g. in the gardens (Kus Veenvliet et al. 2012), and vicinity of bird houses, as ragweed seeds are very often present in packages of sunflower seeds for bird feeding (Strgulc Krajšek and Novak 2013). It is crucial to prevent the development of pollen because of allergies, and to prevent the development of seeds, as their dispersal prolongs the removal problem for many years (Darlington 1922).

Conclusions

1. Only cutting above the 1st pair of leaves (approx. 1.5–3 cm above the ground) has reduced the number of ragweed plants. The observed survival rate was 69%.
2. The cutting reduces the average heights and the average dry mass ragweed plants, regardless of the height of the cut.
3. The cutting reduces the average total lengths of male inflorescences, regardless of the height of the cut.
4. Cutting has almost no influence on the seed (fruit) production. Only the treatment, where plants have been cut above the 2nd pair of leaves, developed significantly less seeds per plant.

Final conclusion: Mowing could reduce the number of surviving plants and the total amount of pollen and seeds, but absolutely not enough. Single mowing is ineffective.

Povzetek

Pelinolistna žvrklja ali pelinolistna ambrozija (*Ambrosia artemisiifolia*) je v Evropi zelo razširjena tujerodna vrsta, ki izvira iz Severne Amerike. V Sloveniji nas k njenemu odstranjevanju zavezuje zakonodaja, ki lastnikom zemljišč zapoveduje odstranjevanje ambrozije in preprečevanje njenega razmnoževanja. Najučinkovitejši način odstran-

jevanja je ruvanje rastlin pred cvetenjem, a ta metoda je časovno potratna in draga, kadar gre za velike sestoje ambrozije. Ker je košnja pogosteje uporabljan način odstranjevanja, smo se odločili izdelati raziskavo o vplivu enkratne košnje na rast in razmnoževanje ambrozije.

Uporabili smo rastline ambrozije, ki smo jih spomladi nabrali ob cesti v predmestju Ljubljane in jih posadili v testna cvetlična korita. Rastline smo na začetku poletja razdelili v 4 skupine po 50 rastlin in jih porezali na treh različnih višinah, kar je predstavljalo košnjo na treh različnih višinah: nad 1., 2. in 3. parom listov. Del rastlin smo pustili neporezanih in so predstavljale kontrolno skupino. Do konca septembra smo spremljali njihovo rast, tako da smo merili višino rastlin, razvoj moških socvetij, v katerih nastaja alergeni pelod, in razvoj semen.

Ugotovili smo, da je propadlo največ rastlin, ki so bile porezane nad prvim parom listov, vse rastline, porezane nad tretjim parom in kontrolne rastline pa so preživele. Najvišje so zrasle kontrolne rastline, ki smo jim na koncu poskusa izmerili tudi največjo suho maso. V nasprotju s pričakovanji so bile razlike v višinah in masi testnih rastlin zanemarljivo majhne. Ugotovili smo tudi, da rastline že v začetku avgusta skoraj dosežejo svojo končno višino, kasneje se rast praktično ustavi in rastlina začne razvijati moška in ženska socvetja.

Že enkratna košnja pred cvetenjem ima velik vpliv na razvoj moških socvetij. Košnja nad 1. in 2. parom listov je skupno dolžino moških socvetij zmanjšala na tretjino, košnja nad 3. parom pa skoraj na polovico. To pomeni veliko zmanjšanje količine alergenega peloda. Skupno največ plodov je zraslo na nepokošenih rastlinah. Ko pa smo izračunali povprečno število plodov na rastlino, se je pokazalo, da se je največ plodov razvilo na kontrolnih in najnižje pokošenih rastlinah. Enkratna košnja torej ne zmanjša tvorbe semen, kar je pomemben podatek za vzdrževalce javnih površin in lastnike zemljišč.

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Symbiotic efficiency, biosorption and the growth of rhizobia on Horse gram plants under aluminium stress

Učinkovitost simbioze, biosorpcije in rasti rizobijev pri vrsti *Macrotyloma uniflorum* zaradi aluminijevega stresa

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Abstract: The aim of the present study was to evaluate the tolerance potential of Horse gram rhizobia to aluminium (Al) toxicity, the enhancement in pod formation, symbiotic efficiency and biosorption potential in the rhizobia inoculated Horse gram (*Macrotyloma uniflorum* (Lam.) Verdc.) plants. Initially, 32 isolates of Horse gram rhizobia were screened for their tolerance of Al in growth media. Among the 32 strains, HGR 4, 6, 13 and 25 that were more tolerant were inoculated individually to Horse gram plants and the plants were then screened for the ability of pod formation, symbiotic efficiency and biosorption potential. Among them, maximum pod formation was observed in Horse gram upon inoculation with HGR-6 and grown at 400 µg g^{-1} of Al. Maximum nodulation was observed in Horse gram upon inoculation with HGR-6 and HGR-13 grown at 200 µg g^{-1} Al. Leghaemoglobin content was maximum on inoculation with HGR-13 at 400 µg g^{-1} of Al. The strain HGR-13 has shown biosorption potential in soil and as well as in root nodules even at 300 µg g^{-1} of Al though it was maximum at 100 µg g^{-1}. This study demonstrated that the Horse gram plants inoculated with *Rhizobium* strains HGR - 4, 6, 13 and 25, besides having nitrogen fixing ability also have the ability to grow in Al contaminated soils. Hence, Horse gram plants associated with these strains of rhizobia could be used in phytoremediation of metal (Al) contaminated soils.

Key words: Aluminium, biosorption, metal tolerance, phytoremediation, *Rhizobium*, symbiotic efficiency.

Izvleček: Namen študije je bil ovrednostiti tolerančni potencial rizobijev za aluminij pri vrsti *Macrotyloma uniflorum* (Lam.) Verdc. Preučevali smo tvorbo strokov, učinkovitost simbioze in biosorpcijski potencial 32 izolatov rizobijev. Med njimi so bili najbolj tolerantni sevi HGR 4, 6, 13 in 25, ki smo jih v nadaljevanju inokulirali individualno na rastline in spremljali 3 parametre. Največjo tvorbo strokov smo izmerili pri sevu HGR-6 in rasti pri 400 µg g^{-1} Al. Največ nodulov je bilo pri inokulaciji s HGR-6 in HGR-13 pri 200 µg g^{-1} Al. Vsebnost leghemoglobina je bila najvišja pri inokulaciji s HGR-13 pri 400 µg g^{-1} Al. Sev HGR-13 je imel biosorpcijski potencial tako v tleh kot v koreninskih nodulih celo pri 300 µg g^{-1} Al, največji pa je bil pri

100 µg g^{-1} Al. Raziskava kaže, da imajo rastline vrste *Macrotyloma uniflorum* , ki so inokulirane s sevi *Rhizobium* HGR - 4, 6, 13 in 25 poleg sposobnosti vezave dušika tudi sposobnost rasti v tleh, onesnaženih z Al. Zato so lahko take rastline primerne za fitoremediacijske postopke s kovinami (Al) onesnaženih tal.

Ključne besede: aluminij, biosorpcija, toleranca za kovine, fitoremediacija, *Rhizobium*, učinkovitost simbioze.

Introduction

Contamination of soils by metals is wide spread due to human, agricultural and industrial activities (Beladi et al. 2011). These activities result in the accumulation of traces of metals in agricultural soils which pose a threat for food safety and public health (Dary et al. 2010). This accumulation of metals leads to loss of soil fertility, since the composition of microbial flora and microbial activities are affected severely (Krujatz et al. 2011). Some metals, though essential in micro-quantities for organisms, are harmful in excess. Aluminium (Al), the third most abundant element in the earth's crust after oxygen and silicon, comprises approximately 7% of its mass (Foy et al. 1978). Al toxicity limits world's agricultural productivity, as Al becomes more soluble in acidic conditions and is the major toxic element in acidic soils and water (Sledge et al. 2005). Excess of Al resists the crop is as a result of direct inhibition of nutrient uptake or impairment in root cell function (Kochaian 1995, Matsumoto 2000) and productivity of plants (Kochian et al. 2004).

Focus on use of legume plants associated with microorganisms for bioremediation of metals is growing everyday (Carrasco et al. 2005). The *Rhizobium*-legume association has an advantage in which both the microorganisms and plants may influence metal solubility, bioavailability. Added to this is an advantage of enhanced nitrogen content of soils when used for bioremediation or phytoremediation (Pajuelo et al. 2008, Dary et al. 2010). Therefore, isolation of rhizobia, capable to tolerate these metal stress is essential for efficient metal remediation and also the nitrogen fixation under metal pollution (Woldeyohannes et al. 2007). The significance in choice of Horse gram for our study is its adaptability to poor adverse climatic conditions, which are unsuitable for other pulse crops. Horse gram is cultivated as a grain legume and fodder crop in the states of Tamil Nadu, Karnataka, Andhra Pradesh and Orissa of South India during Kharif and Rabi (the two agricultural monsoon seasons). Our study targets to analyze the effect of Al tolerant *Rhizobium* strains on pod formation, symbiotic efficiency content and Al biosorption potential of Horse gram plants upon inoculation with the chosen rhizobial strains.

Materials and methods

Isolation and analysis of rhizobial strains

Soil samples were collected from various regions in united Andhra Pradesh, India for sowing the plants. Root nodules were isolated from these plants. Root nodules were surface sterilized and the rhizobial strains were further isolated on Yeast Extract Mannitol (YEM) agar medium (Vincent 1970) with 0.0025% Congo red dye. All these isolates were subjected to biochemical and 16S rRNA sequence analysis. YEM agar medium was prepared with varying concentrations of $Al_2(SO_4)_2$ i.e. 50, 100, 200, 300, 500, 750 and 1000 µg g^{-1}. After solidification, all the isolates were inoculated and incubated at room temperature for 72 hrs. After incubation, the colony diameter was monitored. Replicates were maintained for each metal concentration. Initially 32 isolates of Horse gram rhizobia (HGR's) were screened for the tolerance of aluminium.

Inoculation with rhizobial strains grown under different concentrations of $Al_2(SO_4)_2$

Seeds of Horse gram used during the study were obtained from local fields of Andhra Pradesh, India. The pots of the study were filled with soil sterilized in an autoclave at 121°C for 3 hrs each on three alternative days. Horse gram seeds were surface sterilized with 70% ethanol for 3 min, followed by sodium hypochlorite treatment for 3 min and then rinsed six times with sterilized water, dried. The rhizobial suspension of isolates used in the study were grown in YEM broth in flasks shaken at 120 rpm at 28±2°C for 3 days to obtain a cell density of 6×10^9 cells ml^{-1}. Horse gram plants were inoculated with the selected strains HGR-4 (GQ483457), HGR-6 (GQ483458), HGR-13 (GQ483459) and HGR-25 (GQ483460) which performed well during the initial screening on Al tolerance assay. To perform the inoculations, sterilized seeds were coated with the rhizobial strain by soaking the seeds in liquid culture medium for 2 hrs using 10% (wt/vol) gum Arabic as adhesive to deliver approximately 10^9 cells $seed^{-1}$. Respective controls were maintained with seeds treated in sterilized distilled water. The inoculated seeds (20 seeds pot^{-1}) were sown in clay pots using 2 kg sterilized soil. In order to evaluate the effect of Al metal on the Horse gram plants inoculated with 4 HGR strains, plants were maintained with $Al_2(SO_4)_2$ supplements of 50, 100, 200, 300 and 400 $\mu g\ g^{-1}\ kg^{-1}$. Negative controls were also maintained using the Horse gram plants natively available with $Al_2(SO_4)_2$ supplements of 50, 100, 200, 300 and 400 $\mu g\ g^{-1}\ kg^{-1}$. For the purpose of comparison controls were also maintained without adding Al. Three replicates were maintained for each treatment. The pots were watered regularly and were maintained in an open field conditions and allowed to grow.

Analysis of plants for nodulation, symbiotic efficiency and biosorption potential

The number of pods formed were counted post 40 days of sowing. The plants were observed for nodulation regularly after the seedlings emerged. Five plants in each treatment were picked up randomly and nodulation characteristics were evaluated 40 days after sowing, as it was previously observed during the study that highest nodulation of Horse gram occurred on 40th day. For biochemical analysis, plants raised in different concentrations of Al were collected, the amount of leghaemoglobin was estimated (Tu et al. 1970) post 40 days of sowing. Soil pH, organic matter and total nitrogen (N) (Jackson 1973) and total phosphorus (P) (Olsen et al. 1954) were also estimated. The amount of sand, silt and clay present in the soil were also analyzed (Black 1965).

For elemental analysis, root nodules were collected and washed under tap water to remove sediments and soil. Then they were washed in 0.02% detergent (tween-20) and once again in tap water. They were again washed with 0.1 N HCl. Finaly, the nodules were washed twice with distilled water. The nodules were dried at 80ºC for 48 hrs in hot air oven and they were ground to a very fine powder. From this, 0.5 grams of powdered tissue was added to 5 ml of conc. HNO_3 for cold digestion at room temperature. Then 5 ml of conc. HNO_3 and H_2O_2 were added to the digested sample in 10:4 ratio, the samples were heated to a volume of 2 ml. The clear solution obtained was made up to 25 ml with deionized water (millipore) and used for elemental analysis. Soil samples were also subjected to acid digestion with slight modifications and were used in elemental analysis. Al concentration present in the sample was determined (APHA 22nd Edition, 3111 B) by Atomic Absorption Spectroscopy (AAS) (THERMO AAS Model No: ICE 3000). The system was operated using the Thermo scientific SOLAAR data station V 11.02 software. Argon was used as inert gas during operation. The instrument's operating conditions included Furnace instrumental mode, Lamp current at 15 mA, Wavelength of 232 nm, 0.2 µg/l Gas flow, 0.2 nm band width and 72 sec of Furnace programme total time.

Statistical analysis

Statistical analysis was done in three replicates for each treatment. The mean and standard error (SE) were calculated using Microsoft Office Excel 2007. To test the statistical significance, all the values were analyzed by ANOVA, using SPSS Statistics, Version 20 (Armonk, 2011). Bars indicate means ± SE and were significant at 5% level of significance (P value < 0.05).

Results

Most of the 32 rhizobial isolates were able to grow on YEM agar plates containing 1000 $\mu g\ g^{-1}$ concentration of Al, but the diameter of the colonies varied with the isolate i.e. from 2 mm (HGR-16) to 14 mm (HGR-13). At this concentration the colonies are round, white, translucent, raised and convex with entire margins. Similar results were obtained in YEM broth also. Hence four isolates of the study HGR - 4, 6, 13 and 25 which performed better were further used for evaluation of other parameters.

Al supported good growth of Horse gram plants up to 300 µg g^{-1}, when the plants were inoculated with the four rhizobial strains. Later, the growth of the plants decreased with increase of metal concentration. The plants inoculated with the strains HGR-4, 6, 13 and 25 have shown their maximum pod formation at 100 to 400 µg g^{-1} of Al. Horse gram rhizobial inoculation increased pod formation when compared to control. Among the four selected strains the strain HGR-4 inoculated plants have shown maximum pod formation at 200 µg g^{1}, HGR-6 at 400 µg g^{-1}, HGR-13 at 300 µg g^{-1} and HGR-25 has shown at 100 µg g^{-1} of Al only (Fig. 1). They were significant at 5% level (P value < 0.05).

In the present study, nodules appeared post 13 days of sowing on tap root and as well as on lateral roots at all the Al concentrations experimented. The total number of nodules formed per plant ranged from 8 to 22. The plants inoculated with the strain HGR-6 and 13 have shown highest nodulation at 200 µg g^{-1} of Al. The number of nodules formed were more when rhizobia inoculated to Horse gram plants when compared to control. They were significant at 5% level (P value < 0.05). However, the increased concentration of Al reduced the number of nodules. HGR-4 and 25 inoculated plants had maximum number of nodules at 100 µg g^{-1} of Al only (Fig. 2). The leghaemoglobin content was maximum in the Horse gram plants inoculated with the strains HGR-6 and HGR-13 at 400 µg g^{-1} of Al (Fig. 3). The plants inoculated with HGR-4 and HGR-25 have shown their maximum at 50 µg g^{-1} only. But, these values were more than in control. They were significant at 5% level (P value < 0.05).

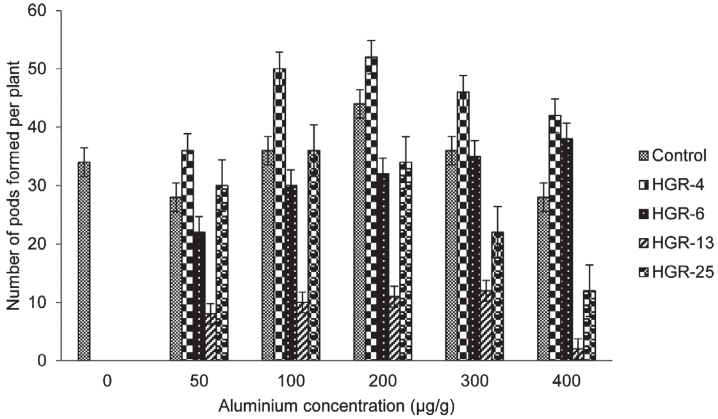

Figure 1: Formation of pods on Horse gram plants inoculated with the four *Rhizobium* strains in response to varying concentrations of aluminium. Data show mean value ± SE.

Slika 1: Tvorba strokov pri rastlinah *Macrotyloma uniflorum,* inokuliranih s štirimi sevi rizobija pri različnih koncentracijah aluminija. Prikazane so povprečne vrednosti ± SN.

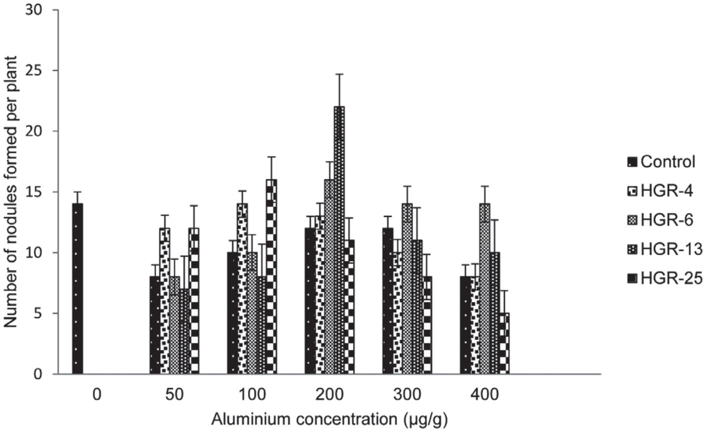

Figure 2: Formation of root nodules on Horse gram plants inoculated with the four *Rhizobium* strains in response to varying concentrations of aluminium. Data show mean value ± SE.

Slika 2: Tvorba koreninskih nodulov pri rastlinah *Macrotyloma uniflorum,* inokuliranih s štirimi sevi rizobija pri različnih koncentracijah aluminija. Prikazane so povprečne vrednosti ± SN.

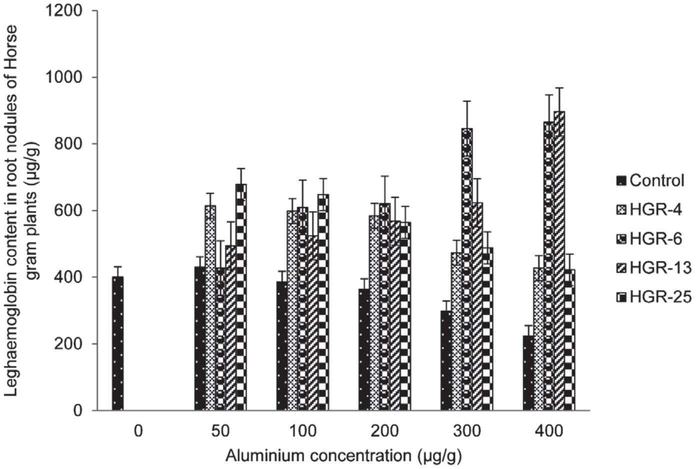

Figure 3: Leghaemoglobin content in root nodules of Horse gram plants inoculated with the four *Rhizobium* strains in response to varying concentrations of aluminium. Data show mean value ± SE.

Slika 3: Vsebnost leghemoglobina v koreninskih nodulih pri rastlinah *Macrotyloma uniflorum,* inokuliranih s štirimi sevi rizobija pri različnih koncentracijah aluminija. Prikazane so povprečne vrednosti ± SN.

The amount of total nitrogen (%) and phosphorus (%) present in the soil is 0.85 and 1.24 respectively. The total content of organic matter in soil is 1.20, sand 18, silt 16, clay 42 and the pH of the soil is 6.44. Among these four strains HGR-13 has shown more number of nodules and maximum leghaemoglobin content at high concentrations of Al. So, we have selected HGR-13 to estimate biosorption potential of the Horse gram rhizobia. Biosorption potential of the strain HGR-13 was

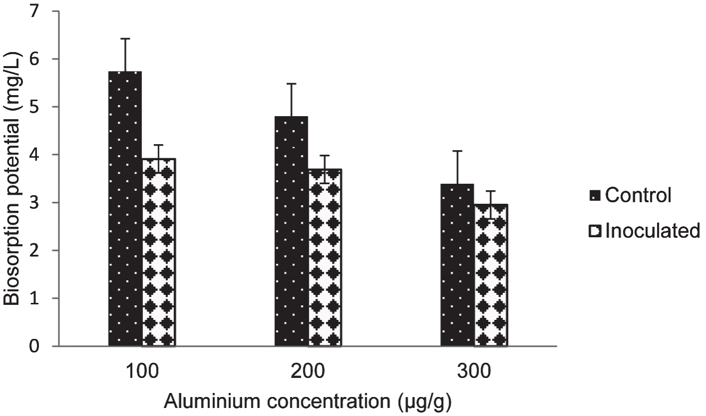

Figure 4: Biosorption potential of the strain HGR-13 in soil after deplantation of Horse gram plants at different concentrations of aluminium. Data show mean value ± SE.

Slika 4: Biosorpcijski potencial seva HGR-13 po presaditvi rastlin *Macrotyloma uniflorum,* v tla z različno koncentracijo aluminija. Prikazane so povprečne vrednosti ± SN.

determined by Atomic Absorption Spectroscopy (AAS), as the amount of metal present in the nodule and soil samples after the treatment with the isolate HGR-13. After analyzing the treated samples in AAS, the inoculated strain HGR-13 has shown maximum biosorption of Al. The results have shown that the Al present in the soil was decreased after deplantation of Horse gram plants when they were inoculated with the Al tolerant rhizobia (HGR-13) i. e. from 5.74 mg/L (control without inoculation) to 3.91 mg/L at 100 µg g^{-1}, 4.8 mg/L to 3.69 mg/L at 200 µg g^{-1} and 3.39 mg/L to 2.95 mg/L at 300 µg g^{-1} of Al concentration. In nodules, the biosorption potential was maximum at 200 µg g^{-1} (1.69 mg/L to 0.99 mg/L), at 100 µg g^{-1} it was 1.92 mg/L to 1.89 mg/L and at 200 µg g^{-1} it was 1.28 mg/L to 1.27 mg/L. The results have shown that the isolate was able to adsorb Al at a concentration of 300 µg g^{-1} in root nodules and also in soil samples inoculated with the strain HGR-13 (Fig. 4, 5).

Discussion

In our study all the tested Horse gram rhizobia are able to show growth at all the Al concentrations tested. But, they have shown variations in their growth. Al stress reduced the growth of rhizobial species under laboratory conditions and also in natural environment (Paudyal et al. 2007; Avelar Ferreira et al. 2012). Some cowpea rhizobia tolerate up to 20 m mol_c dm^{-3} of Al^{+3} (Bruno et al. 2013). *Rhizobium* species like *Sinorhizobium meliloti* and *Bradyrhizobium* growing explanta were extremely sensitive to Al (Arora et al. 2001). The rhizobia from Bambara groundnut were able to grow in a medium pH as low and Al concentration of 50 µM (Laurette et al. 2015). The growth of the *Rhizobium* strain CB756 was also not affected by 50 µM Al at pH 4.5 (Keyser and Munns, 1979). But 50 µM Al at pH 4.6 decreased the growth of *Bradyrhizobium* spp. (Shamsuddin 1987) and the growth of rhizobia was completely inhibited at 50 mM Al (Broos et al. 2004). At high concentrations Al is a potent inhibitor of rhizobial growth. It was observed that root nodule bacteria grow after a lag period in culture medium containing 75 µM Al (Whelan and Alexander 1986). Wild rhizobia from Soybean have shown growth at 200 µ $mol.L^{-1}$ of Al^{3+} (Ping et al. 2014). It has shown negative effect on the survival and growth of *Rhizobium trifolii*. *Bradyrhizobium* strains were able to show growth in the presence of 100 µM $AlCl_3$ (Lesueur et al. 1993) and some *Bradyrhizobium japonicum* strains were tolerant to Al (Tayler et al. 1991).

Anoxybacillus sp. SK 3-4 was found to be the most resistant to Al and significant growth was observed at 300 mg L^{-1} to 800 mg L^{-1} of Al (Lim et al. 2015). To the best of our knowledge this is the first report that rhizobia nodulating Horse gram were able to grow in culture medium containing 1000 µg g^{-1} Al concentration.

Al effects the growth and nodulation of many legumes (Kim et al. 1985). Kushwaha et al. 2017 observed in a study with cowpea, the number of pods formed were more in soil upon treatment with 40 ppm concentration of Al. In the present study the number of pods formed was more at 100 to 400 µg g^{-1} of Al. The inoculation of acid tolerant, Al tolerant *Bradyrhizobium japonicum* strains could increase number of pods in soybean (Situmorang et al. 2009). Previous studies reported that at high Al concentrations, nodulation was partially or totally inhibited in several species such as common bean (*Phaseolus vulgaris*), clover (*Trifolium repens*), *Stylosanthes* species and also in other tropical legumes (de Carvalho et al. 1981, Paudyal et al. 2007). de Carvalho et al. 1981 reported that Al has shown its effect on reduction or inhibition of nodulation at 25 iM concentration. Kushwaha et al. 2017 during their study reported that the more number of nodules formed at lower concentrations of Al (0 and 20 ppm) and number of nodules were reduced at higher concentration of Al. Brady et al. 1990 reported that Al at < 5 µM has shown reduction in nodulation of soybean. Inoculation of *Sinorhizobium mexicanum* ITTG 27^T to *Acaciella angusstissime* plants enhanced nitrogen content (Rosales et al. 2011). Al toxicity has shown negative effect on symbiotic nitrogen fixation in common bean plants that were grown hydroponically in acidic nutrient solution containing 70 µM $AlCl_3$ (Mendoza-Soto et al. 2015). Blamey and Chapman, 1982 reported that in groundnut, poor nodulation and nitrogen fixation was observed under Al toxicity. Horse gram rhizobia i.e. HGR-6 and HGR-13 inoculated plants have shown increased leghaemoglobin content even under 400 µg g^{-1} of Al stress. de Carvalho et al. 1982 suggest that the effects of Al on N_2 fixation may be indirect. The rhizospheric microorganisms have intrinsic ability to reduce/detoxify the metal stress by several mechanisms. These mechanisms include the efflux of metal ions outside the cell, biostimulation, bioaugmentation, metal reduction and biosorption (Outten et al. 2000). Mammaril et al. 1997 proved that the metal concentration decreased after rhizobial inoculation, which shows the ability of their rhizobial strain RP5 in the removal of metals through adsorption-desorption mechanism. Bacterial biosorption/bioaccumulation mechanisms together with other plant growth promoting features accounted for improved plant growth in metal contaminated soils (Zaidi et al. 2006). Horse gram rhizobia (HGR-13) have the ability to remove Al even at 300 µg g^{-1} Al, even though it was maximum at 100 µg g^{-1} in the inoculated plants when compared to control plants. Hence, rhizobia nodulating their hosts may increase metal accumulation in root nodules and may lead to chelation, immobilization and biosorption (Hao et al. 2014).

Conclusions

Results clearly show that the accumulation of Al in soils reduced upon inoculation of Horse gram plants with Horse gram rhizobia of the current study. The present study demonstrated that the Horse gram plants inoculated with Al tolerant *Rhizobium* strains HGR-4, 6, 13 and 25 besides having nitrogen fixing capacity also have the ability to grow in Al contaminated soils. Hence, these Horse gram plants upon inoculation of the rhizobia associated with them during the study i. e HGR 4, 6, 13 and 25 could be used in phytoremediation of metal from Al contaminated soils.

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Accessibility of school health education is an underlying factor for differences in knowledge about sexually transmitted infections of secondary school pupils

Dostopnost do šolske zdravstvene vzgoje pogojuje razlike v znanju dijakov o spolno prenosljivih okužbah

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Abstract: Health education constituted an individual subject in secondary schools in Slovenia before 1985. Thereafter it was disintegrated and its topics incorporated into different school subjects. Health education topics are required in the extent of 15 hours in upper secondary general education schools, but in the extent of 0 to 18 hours in other secondary school programmes. The present study compared the knowledge about sexually transmitted infections of pupils of two 4-year secondary school programmes with different health education requirements. The results demonstrated that different accessibility of school health education results in distinct differences in knowledge about the existence, sources of infection, symptoms, and protection against sexually transmitted infections between pupils of different secondary school programmes. Despite the general conception of overloaded curriculums, more than two thirds of pupils of both educational programmes expressed the need of receiving more information in sexual education topics, with systematic medical exam selected as the most suitable form of sexual education, closely followed by Biology class, and school project day. The results call for the attention of educational policy makers, as they clearly emphasise the need of establishing systematic and comprehensive school health education for all pupils, not only for those enrolled in the selected secondary school programmes.

Key words: sexually transmitted infections, sexual education, health education, secondary education

Izvleček: Pred letom 1985 je bila zdravstvena vzgoja samostojen srednješolski predmet. Kasneje so bile njene vsebine vključene v različne šolske predmete. Za srednje splošno izobraževanje je danes predpisanih 15 ur obveznih vsebin zdravstvene vzgoje, za druge srednješolske programe pa od 0 do 18 ur. Pričujoča raziskava je primerjala znanje o spolno prenosljivih okužbah dijakov dveh 4-letnih srednješolskih programov z različnim obsegom zdravstvene vzgoje. Rezultati raziskave so pokazali, da se različna dostopnost do šolske zdravstvene vzgoje srednješolcev odraža v izrazitih razlikah v poznavanju spolno prenosljivih okužb in v znanju dijakov o virih okužbe, simptomih in zaščiti pred spolno prenosljivimi okužbami. Kljub splošni predstavi o prenasičenih predmetnikih, je več kot dve tretjini dijakov obeh srednješolskih programov izrazilo potrebo po večjem obsegu spolne vzgoje, pri čemer so kot najbolj primerno obliko za spolno vzgojo izbrali sistematski zdravniški pregled, takoj za tem pa ure biologije in šolski projektni dan. Rezultati kličejo po pozornosti oblikovalcev izobraževalne politike, saj so jasno pokazali potrebo po vzpostavitvi sistematizirane in izčrpne zdravstvene vzgoje za vse dijake, ne le za dijake izbranih srednješolskih programov.

Ključne besede: spolno prenosljive okužbe, spolna vzgoja, zdravstvena vzgoja, srednješolsko izobraževanje

Introduction

World Health Organisation (WHO) defines sexual health as a state of physical, emotional, mental, and social well-being in relation to sexuality; sexual health is thus not merely the absence of disease, dysfunction or infirmity (World Health Organization 2006). According to WHO, the ultimate objective of sexual health is thus the attainment of physical, emotional, mental, and social well-being in relation to sexuality, with comprehensive education and information being one of the crucial sexual health intervention areas (World Health Organization 2017).

In Slovenian educational system (Direktorat… 2019), sexual education is part of health education topics. These topics constituted an individual subject in secondary schools before 1985, but were afterwards disintegrated and incorporated into different subjects, including Biology and Civil education and ethics in primary schools, and Compulsory elective topics in secondary schools.

In Slovenia, the extent of obligatory health education topics is equal for pupils of all primary schools. In secondary schools, however, the extent of obligatory health education topics varies between different school programmes. Consequently, health education topics have the extent of 15 hours in Upper secondary general education schools (for example: general high school graduate programme), from 0 (for example: electrician programme) to 18 hours (for example: mechanical technician programme) in Upper secondary technical education schools, 0 hours in Upper secondary vocational education schools (for example: hairdresser programme, auto mechanic programme), and 6 hours in Short upper secondary vocational education schools (for example: carpenter programme) (Obvezne izbirne vsebine… 2015). Thus, although recognised as a critical part of sexual health intervention areas by the WHO (World Health Organization 2017), it is clearly evident that comprehensive health education is not equally available to all secondary school pupils in Slovenia. We therefore hypothesised that these differences in the accessibility of health education between pupils enrolled in different secondary school programmes will be reflected in their knowledge about sexually transmitted infections.

Material and methods

Pupils of two 4-year secondary school programmes were invited to voluntarily participate in the study. Pupils of three classes of the fourth year of the Novo mesto grammar school (which is an upper secondary general education programme) (school A), as well as pupils of three classes of the fourth year of electrician programme of Secondary electro school and technical gymnasium of School centre Novo mesto (which is an upper secondary technical education programme) (school B) participated in the study. Fifteen hours of health education, which are presented during Biology classes, are included in the curriculum of school A pupils, but none in the curriculum of school B pupils. In addition, pupils of school A have obligatory classes of Biology for two hours per week in the first three years of schooling, and selective four to six hours per week of Biology in their fourth year of schooling; pupils of school B do not have any classes of Biology during their four years of schooling.

An anonymised online questionnaire relating to the knowledge about sexually transmitted infections was prepared for all pupils with an online open-source tool 1ka (https://www.1ka.si/). Twenty-five mainly closed questions were included in the questionnaire and were aimed to assess the knowledge of pupils about the existence, sources of infection, symptoms, and protection against sexually transmitted infections, as well as about their acquaintance with the existing publically accessible professional sexual education projects, and their experiences and wishes regarding sexual education.

The questionnaires were completed by the pupils anonymously, in the computer classrooms in schools during regular course time. While the pupils were answering the questionnaire, investigator was available in the same classroom to answer any technical- or subject-related questions.

The collected data were transferred from the online questionnaire into Microsoft Excel 2010 (Microsoft Office 2010), examined and analysed. All data were divided into those obtained from pupils of school A and those obtained from pupils of school B. A Chi-square test was applied to determine any statistically significant differences between the two groups. Level of <0.05 was adopted as statistically significant.

Results

The questionnaire was fulfilled by 50 pupils of school A and 71 pupils of school B. Among males, there were 28 females who fulfilled the questionnaire in school A, and no females among those who answered the questionnaire in school B. The average (standard deviation) age of the participating pupils was 18 (0.21) years.

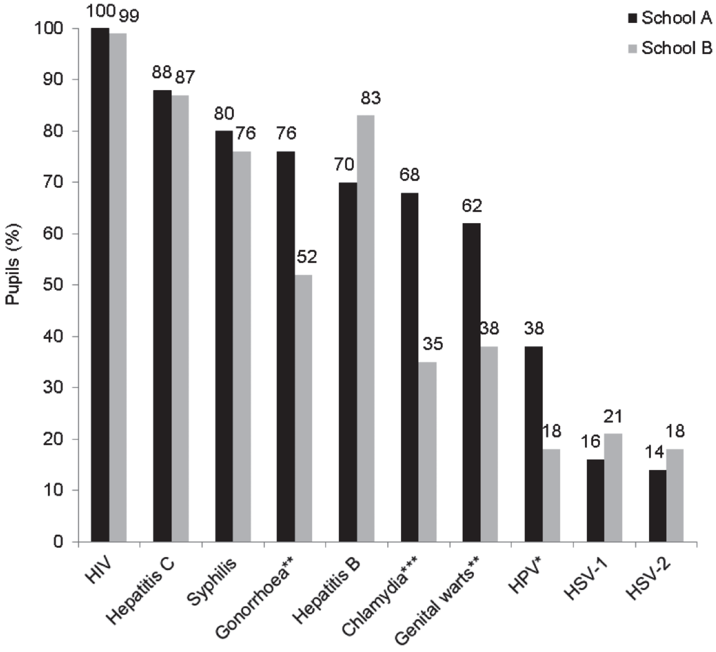

Figure 1: The percentage of pupils from a given secondary school programme that selected a given sexually transmitted infection as the one for which they had already heard of. School A - upper secondary general education programme, School B - upper secondary technical education programme. HIV - human immunodeficiency viruses, HPV - human papilloma virus, HSV 1 - herpes simplex virus type 1, HSV 2 - herpes simplex virus type 2. Asterisks mark statistically significant differences between the pupils of the two secondary school programmes (* p <0.05, ** p <0.01, *** p <0.001).

Slika 1: Odstotek dijakov posamezne srednje šole, ki so določeno spolno prenosljivo okužbo izbrali kot tisto, ki jo poznajo. Šola A – splošni program srednje šole, Šola B – tehniški program srednje šole. HIV – humani virusi imunske pomanjkljivosti, HPV – humani papiloma virus, HSV 1 – virus herpes simplex tipa 1, HSV 2 – virus herpes simplex tipa 2. Zvezdica označuje statistično značilno razliko med dijaki obeh srednješolskih programov (* p <0.05, ** p <0.01, *** p <0.001).

Of 121 participating pupils, 71% reported that they were already sexually active, with no statistically significant differences (p >0.05) observed between the pupils of the two schools (68% in school A, 73% in school B).

The most interesting results, obtained from the answers of pupils, are presented below.

Pupils had to select the sexually transmitted infections that they had already heard of. The majority of pupils reported they had heard of HIV (human immunodeficiency virus), syphilis, and hepatitis (both B and C) (Figure 1). Far less of them reported they had heard of gonorrhoea, chlamydia, genital warts, HPV (human papilloma virus), and HSV (herpes simplex virus, both type 1 and 2). Statistically significant differences were observed between the results of pupils of the two schools, with constantly lower values observed in pupils of School B (Figure 1).

When asked about the common symptoms of sexually transmitted infections, a high percentage of pupils from both schools A (92%) and B (89%)

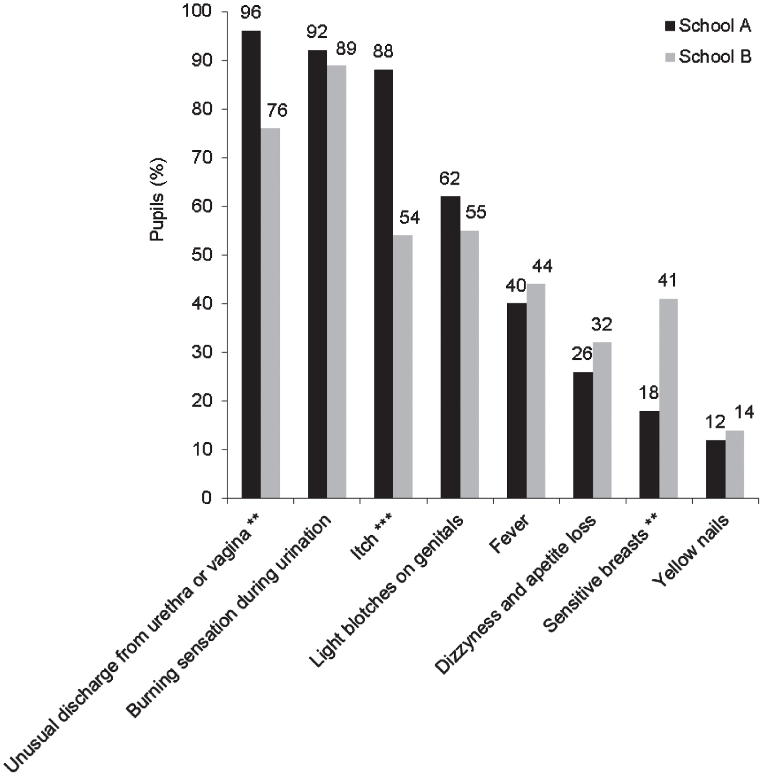

Figure 2: The percentage of pupils from a given secondary school programme that selected a given symptom as a common symptom of a sexually transmitted infection. Only the first three answers from left to right are correct, i.e. are actual symptoms of an infection. School A - upper secondary general education programme, School B - upper secondary technical education programme. Asterisks mark statistically significant differences between the pupils of the two secondary school programmes. * p <0.05, ** p <0.01, *** p <0.001

Slika 2: Odstotek dijakov posamezne srednje šole, ki so določen simptom izbrali kot pogost simptom spolno prenosljive okužbe. Pravilni (t.j. dejanski simptomi spolno prenosljive okužbe) so prvi trije odgovori na levi strani. Šola A – splošni program srednje šole, Šola B – tehniški program srednje šole. Zvezdica označuje statistično značilno razliko med dijaki obeh srednješolskih programov (* p <0.05, ** p <0.01, *** p <0.001).

selected the correct symptom of burning sensation during urination, with no statistically significant differences between the two groups. However, a significantly smaller number of pupils from school B than from school A selected unusual discharge from urethra or vagina (76% vs. 96%; $p < 0.01$) and itch (54% vs. 88%; $p < 0.001$) as the two other correct common symptoms of sexually transmitted infections. In addition, significantly more pupils (41% vs. 18%; $p < 0.01$) from school B than from school A incorrectly selected sensitive breasts as a common symptom of sexually transmitted infection. Several pupils from both schools A and B also selected the other incorrect statements about common symptoms of sexually transmitted infections as correct (Figure 2).

Seven percent of pupils from School B, but none from school A ($p < 0.05$) incorrectly stated that contraceptive pills can provide effective prevention against sexually transmitted infections. Similarly, 4% of pupils from school B, but none from school A ($p < 0.05$) incorrectly stated that in case of sexually transmitted infection one should ask for antibiotics in a pharmacy. Also, 45% of pupils from school B, but 10% from school A ($p < 0.001$) incorrectly stated that in case of HIV infection no treatment is available, the others selected antiretroviral drugs as available treatment. In addition, 41% of pupils from school B and 14% of pupils from school A ($p < 0.001$) incorrectly stated that HIV infection is a bacterial infection.

Ninety percent of pupils from school B and 82% of those from School A ($p > 0.05$) did not participate in any of the stated publically accessible professional sexual education projects. Even more, almost a half of pupils (49%) from school B and 30% of pupils from school A did not hear for any of the publically accessible professional sexual education projects (Figure 3). At the same time, more than three quarters (78% and 82%,

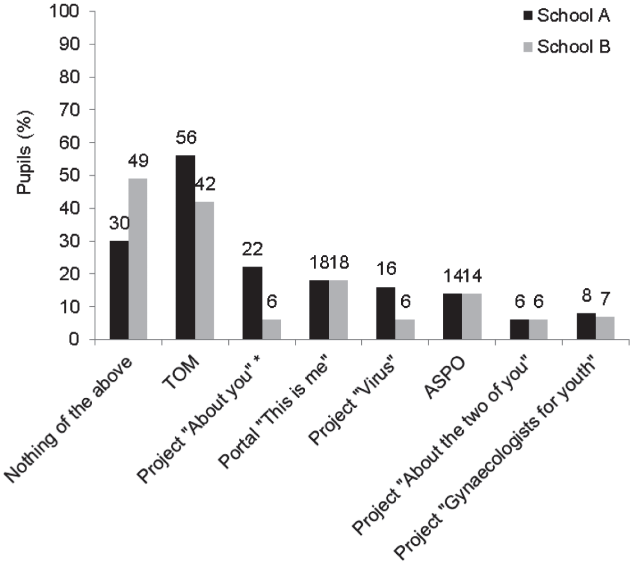

Figure 3: The percentage of pupils from a given secondary school programme that selected a given publically accessible professional sexual education projects as familiar. School A - upper secondary general education programme, School B - upper secondary technical education programme. TOM - telephone for children and youth, ASPO - online application for recognition and information about sexually transmitted infections.

Slika 3: Odstotek dijakov posamezne srednje šole, ki so določen javno dostopen izobraževalni projekt s področja spolne vzgoje izbrali kot tistega, ki ga poznajo. Šola A – splošni program srednje šole, Šola B – tehniški program srednje šole. TOM – telefon za otroke in mladostnike, ASPO – spletna aplikacija za prepoznavanje in informiranje o spolno prenosljivih okužbah.

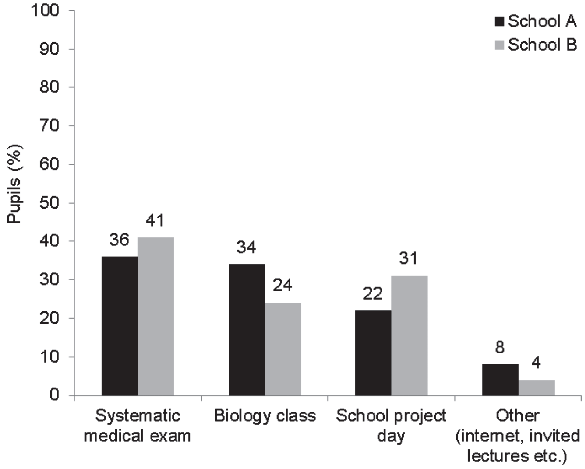

Figure 4: The most suitable forms of sexual education, as selected by the pupils of upper secondary general education programme (School A) and upper secondary technical education programme (School B).

Slika 4: Najprimernejše oblike spolne vzgoje po izboru dijakov srednjega splošnega izobraževanja (gimnazija) (Šola A) in srednjega strokovnega izobraževanja (program elektrotehnik) (Šola B).

pupils from school A and B, respectively; p >0.05) provided positive feedback when one of these (ASPO, *n.d.*) was presented to them.

In addition, regardless that health education topics required by law in some of the secondary school programmes, of which sexual education should be a part of, there were 20% of pupils from school B and 2 % of pupils from school A (p <0.05) who reported that they had not participated in any of the sexual education topics throughout their secondary school education. Additional 48% of pupils from school B and 66% of pupils from school A (p <0.05) reported to participate in only 1 to 5 hours of sexual education topics throughout their secondary school education. We found it interesting that 28% and 20% of pupils from school A and B, respectively, stated that they had not asked any questions during their sexual education, not because they did not have any, but because they were ashamed. In case they would have had the opportunity to ask questions anonymously in advance, 70% of pupils from school A and 61% of pupils from school B stated they would have actually posed a question.

Last but not least, more than two thirds (i.e. 78% of pupils from school A and 68% of pupils from school B; p >0.05) stated they would require more sexual education topics through the course of their education, with systematic medical exam selected as the most suitable form, closely followed by Biology class, and school project day (Figure 4).

It is also worth stressing that individual suggestions received from several students called for the inclusion of not only biological/physiological topics and topics related to sexually transmitted infections into sexual/health education, but also for the inclusion of psychological and emotional dimensions that would help establishing a positive and respectful approach to sexuality.

Discussion

The results of the present study demonstrate that the accessibility of school health education significantly affects the knowledge about sexually transmitted infections of secondary school pupils. Clear lack of knowledge about sexual education topics was observed in pupils of upper secondary technical education programme (school B) when compared to pupils of upper secondary general education programme (school A). This difference in knowledge between pupils of the two schools was consistent along all the posed questions in which statistically significant differences were observed. Pupils of Upper secondary technical education programme (school B) demonstrated significantly lower knowledge about the existence, sources of infection, symptoms, and protection against sexually transmitted infections. Although the sample of secondary school pupils in the present study was rather small, the observed differences are far too profound and far too consistent to be of random nature.

Nevertheless, we can not exclude the possibility that gender structure of the two programmes might have been a contributing factor to the observed results. Namely, in the Upper secondary general education programme half of the participating pupils were females, who often have higher school grades than males, while there were only male pupils in the Upper secondary technical education programme. However, as the available sample does not allow gender analysis relative to educational programme, this option can not be tested. In addition, it would be beneficial, if school grades of the participating pupils would be available, so that the potential correlation between school success and knowledge about sexually transmitted diseases could be tested, but, as anonymity was guaranteed, these data were not available in the present study.

According to the existing curriculums of the two educational programmes, 15 hours of health education are obligatory for pupils of school A, but no health education is obligatory for pupils of school B during their four years of secondary schooling. Sexual education is one of the crucial parts of health education topics, yet 68% of pupils of both schools reported to participate in a maximum of 5 hours of sexual education during the course of their schooling, with a fifth of pupils from school B who reported receiving no sexual education at all.

Comprehensive sexual education consists of accurate, age-appropriate and up-to-date information on physical, psychological, and social aspects of sexuality and reproduction, as well as sexual and reproductive health and ill health (World Health Organization, 2017). Effective sexual education, combined with easy access to contraception, can effectively reduce adolescent pregnancy rates (Speroff and Darney 2005, cit. in Fuller 2007). Also, accurate and comprehensive information can build positive attitudes and values, and healthy behaviour (World Health Organization, 2017). As for the above results, not all of the Slovenian pupils have the access to school health education, which decreases the likelihood of adolescents making well informed choices.

We find it particularly concerning that, despite rather intense publicity, one can still find teenaged individuals, who are not familiar with HIV infection. Also, only a third of pupils of Upper secondary technical education programme selected chlamydia as sexually transmitted infection for which they had already heard of, despite the fact that chlamydia is the third most often reported sexually transmitted infection in Slovenia (Sočan et al. 2018). It is not to be neglected that the incidence of infections with chlamydia has been increasing in both genders over the last ten years, with the highest incidence observed in young people (Sočan et al. 2018). This is not coincidental, as young people up to the age of 25 are a group with the highest-risk for sexually transmitted infections, as they usually change their sexual partners more often than older people (Pinter 2010). Results of a national HBSC study from 2014 suggest that 20% of 15-year old adolescents were already sexually active, with a quarter of them not using protection (Jeriček Klanšček 2015). Apart from chlamydia, an increase in sexually transmitted infections over the last ten years in Slovenia has also been observed for genital warts and gonorrhoea (Sočan et al. 2018), for which only a third and a half of pupils of upper secondary technical education programme, respectively, had heard of.

In addition, pupils from both schools declared a rather poor acquaintance with the existing publically accessible professional sexual education projects. Their generally positive feedback to the presentation of one of such projects (ASPO, *n.d.*) suggests, however, that they require receiving more information. This is additionally supported by the fact that substantially more than two thirds of pupils expressed support for the inclusion of more sexual education topics in the existing curriculum, with some of them expressing the wish of health/sexual education being established as an individual subject, which is in clear contrast to a general perception of overloaded secondary school curriculum.

The pupils of both educational programmes clearly expressed the need of receiving more information in sexual education topics, as around two thirds of pupils of both schools declared they would have posed a question related to sexual education, if only they had had the opportunity of doing so in advance and anonymously. This result demonstrates that it can not be stressed enough, how important it is for sexual education providers to establish a respectful and safe environment for the pupils, when these topics are being presented.

Conclusions

The present study demonstrated the importance of school health education for adolescents and revealed that the accessibility to school health education is an underlying factor for the observed differences in knowledge about sexually transmitted infections between pupils of different 4-year secondary school programmes. Ideally, educational policy makers would recognise the importance of health education for all youngsters, not only for those enrolled in selected secondary school programmes, and would consequently re-establish its position among obligatory school subjects. A less demanding task would be to include obligatory hours of health education into all secondary school programmes; positive feedback from pupils suggests such implementation would not face any serious resistance. Finally, a more systematic approach to health education, including a systematic presentation of the already existing publically accessible professional sexual education projects, would increase its effects and empower pupils for a self-motivated evidence-based self-education and making of well informed choices.

Povzetek

Svetovna zdravstvena organizacija (WHO) izčrpno spolno vzgojo postavlja za temelj intervencij na področju spolnega zdravja (World Health Organization 2017), ki je definirano ne le kot odsotnost bolezni, pač pa kot stanje s spolnostjo povezanega fizičnega, čustvenega, miselnega in socialnega blagostanja (World Health Organization 2006). Pred letom 1985 je bila zdravstvena vzgoja v Sloveniji samostojen srednješolski predmet, kasneje pa so bile njene vsebine vključene v različne šolske predmete.

Za srednje splošno izobraževanje je danes predpisanih 15 ur obveznih vsebin zdravstvene vzgoje, za druge srednješolske programe pa od 0 do 18 ur. Pričujoča raziskava je primerjala znanje o spolno prenosljivih okužbah dijakov dveh 4-letnih srednješolskih programov (splošne gimnazije in programa elektrotehnik) z različnim obsegom zdravstvene vzgoje. V raziskavo je bilo vključenih 121 dijakov prostovoljcev, 50 dijakov 4. letnika gimnazije in 71 dijakov 4. letnika programa elektrotehnik. Vsi dijaki so v šolski računalniški učilnici ob prisotnosti anketarja anonimno izpolnili vprašalnik z vprašanji o spolno prenosljivih okužbah, ki smo ga oblikovali v odprtokodnem spletnem orodju 1ka.

Rezultati so pokazali na dosledne razlike v znanju med obema skupinama dijakov, pri čemer so dijaki programa elektrotehnik značilno slabše poznali spolno prenosljive okužbe, njihove simptome in zaščito pred spolno prenosljivimi okužbami kot njihovi vrstniki gimnazijci. Znatno manj dijakov programa elektrotehnik kot gimnazijcev je poznalo okužbo s klamidijo in gonorejo, ki sta poleg genitalnih bradavic spolno prenosljivi okužbi, ki sta v zadnjih desetih letih v Sloveniji v porastu, pri čemer je njuno največjo incidenco zaslediti ravno med mladimi (Sočan et al. 2018).

Kljub splošni predstavi o prenasičenih predmetnikih, je več kot dve tretjini dijakov obeh srednješolskih programov izrazilo potrebo po večjem obsegu spolne vzgoje, pri čemer so kot najbolj primerno obliko za spolno vzgojo izbrali sistematski zdravniški pregled, takoj za tem pa ure biologije in šolski projektni dan. Izpostaviti velja tudi, da je več kot petina dijakov obeh srednješolskih programov navedla, da med urami spolne vzgoje niso postavili vprašanja, ne zato, ker ga ne bi imeli, pač pa zato, ker jih je bilo sram. Obenem je dve tretjini dijakov navedlo, da bi vprašanje postavili, če bi to lahko storili anonimno vnaprej. Izvajalci spolne vzgoje bi se morali torej dobro zavedati, kako velik je pomen vzpostavitve varnega in spoštljivega okolja za učinkovito izvedbo spolne vzgoje. Dijaki so obenem navedli, da si pri izvedbi spolne vzgoje poleg bioloških/fizioloških vsebin in vsebin, povezanih s spolno prenosljivimi okužbami želijo slišati tudi sovpadajoče psihološke in čustvene vsebine, ki bi pomagale pri vzpostavljanju pozitivnega in spoštljivega pristopa do spolnosti.

Rezultati pričujoče raziskave kličejo po pozornosti oblikovalcev izobraževalne politike, saj se je jasno pokazala potreba po vzpostavitvi sistematizirane in izčrpne zdravstvene vzgoje za vse dijake, ne le za dijake izbranih srednješolskih programov.

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8. kongres evropskih mikrobiologov – FEMS 2019

8th Congress of European Microbiologists – FEMS 2019

7. - 11. julij 2019, Glasgow, Škotska

8. kongres evropskih mikrobiologov, ki je letos potekal na Škotskem v Glasgow-u, je zagotovil pisano mednarodno zasedbo s predavatelji iz kar 23 držav. V okviru srečanja se je zvrstilo šest plenarnih predavanj, čemur je sledilo kar 32 simpozijev, 24 delavnic ter ducat posebnih sekcij. Istočasno tekom kongresnega dneva je potekalo kar osem znanstvenih sekcij, ki so pokrivale širok nabor mikrobioloških tem. V treh dneh je bilo na ogled preko 1300 posterjev. Slovenska udeležba na kongresu tudi ni bila nezanemarljiva, saj so se ga udeležili mikrobiologi z Biotehniške fakultete Univerze v Ljubljani, Medicinske fakultete Univerze v Ljubljani, Klinike Golnik, Znanstveno-raziskovalnega centra SAZU in Univerze na Primorskem. Na srečanju si je prav gotovo vsak udeleženec osvežil znanje pa tudi spoznal veliko novosti in trendov.

Pestre mikrobne metabolne poti še vedno presenečajo, vendar se jih vedno bolj izkorišča in prilagaja za potrebe pridobivanja industrijskih in farmacevtskih snovi, vključno z anorganskimi materiali. Nova spoznanja o malih regulatornih RNA molekulah že omogočajo pridobivanje visokih koncentracij metabolitov v nekaterih biotehnoloških postopkih.

Razvijajo se številne molekularne aplikacije CRISPR-Cas imunskega sistema pri bakterijah, kar vključuje (in)aktivacije genov ter modifikacije genomov tako pri prokariontih kot evkariontih. Bioinformatična analiza je pokazala, da pri bakteriji lahko obstaja 28 obrambnih sistemov proti bakteriofagom. Na drugi strani pa je dokazan obstoj številnih genov anti CRISPR, ki so lahko vključeni v DNA bakteriofagov, transpozonov in plazmidov. Izmenjava genetskega materiala tako v naravi kot laboratoriju, vloga epigenetike in proučevanje rezistoma je pomembno pri razumevanju širjenja antibiotičnih rezistenc. Po zaužitju antibiotika vankomicina pri ljudeh se v kar pri 90% bolnikov ne povrne prvotna sestava črevesnega mikrobioma. To je pomembna informacija tudi v smislu razumevanja hitrega prehajanja bakterijskih snovi, npr. peptidoglikana iz človekovega črevesja neposredno v krvni obtok.

Vedno bolj razumemo mehanizme patogeneze številnih patogenov in njihov vpliv na gostiteljsko celico, kar npr. pri listeriji vključuje fragmentacijo mitohondrijev, reorganizacijo citoskeleta, spremenjene genske espresije gostiteljske celice in imunskega odgovora napadenega organizma. Od komenzala do parazita je samo en korak oziroma ena molekula, kot so to dokazali v primeru kandide oziroma toksina kandidalizina, ki lahko deluje kot virulenčni ali antivirulenčni dejavnik, odvisno od okolja oziroma okoljskega tkiva gostitelja.

Sociomikrobiologija postaja vedno pomembnejša v smislu razumevanja socialnih interakcij pri mikroorganizmih, organizaciji kompleksnih mikrobnih komunikacijskih poti, sposobnosti spreminjanja fenotipov, pa tudi žrtvovanja dela bakterijske populacije za dobrobit ohranjanja drugega dela populacije in z njo povezano genetsko zalogo.

Avtotrofija (fiksacija ogljikovega dioksida) je v bakterijskem svetu precej bolj razširjena kot je še do nedavnega veljalo, kar bo marsikje spremenilo naš dosedanji pogled na ekosistem in klimatske spremembe. Počasi razumevamo vlogo fenolega pigmenta purpurogallina, ki ga imajo alge, ki povzročajo nastanek »umazanega ledu« na Grenlandiji in s tem povezanega hitrejšega učinka taljenja ledu.

FEMS (Federation of European Microbiological Societies) pa ne vključuje samo organiziranja kongresov, ampak daje raziskovalcem tudi podporo za udeležbe na srečanjih in znanstvenih izmenjavah ter organizira izobraževanja, npr. poletne šole. Postaja zelo pomembna platforma za ustvarjanje povezav in izmenjavo informacij. FEMS izdaja tudi več revij (FEMS Microbiology Ecology, FEMS Microbiology Reviews, FEMS Microbiology Letters, FEMS Yeast Research, Pathogens and Disease), ki se jim bosta v kratkem pridružile še dve novi. Slovensko mikrobiološko društvo (SMD) je eno izmed 52 članov FEMS-a. Naslednji kongres FEMS bo od 11. do 15. julija 2021 v Hamburgu v Nemčiji.

Janez Mulec

INSTRUCTIONS FOR AUTHORS

1. Types of Articles

SCIENTIFIC ARTICLES are comprehensive descriptions of original research and include a theoretical survey of the topic, a detailed presentation of results with discussion and conclusion, and a bibliography according to the IMRAD outline (Introduction, Methods, Results, and Discussion). In this category ABS also publishes methodological articles, in so far as they present an original method, which was not previously published elsewhere, or they present a new and original usage of an established method. The originality is judged by the editorial board if necessary after a consultation with the referees. The recommended length of an article including tables, graphs, and illustrations is up to fifteen (15) pages; lines must be double-spaced. Scientific articles shall be subject to peer review by two experts in the field.

REVIEW ARTICLES will be published in the journal after consultation between the editorial board and the author. Review articles may be longer than fifteen (15) pages.

BRIEF NOTES are original articles from various biological fields (systematics, biochemistry, genetics, physiology, microbiology, ecology, etc.) that do not include a detailed theoretical discussion. Their aim is to acquaint readers with preliminary or partial results of research. They should not be longer than five (5) pages. Brief note articles shall be subject to peer review by one expert in the field.

CONGRESS NEWS acquaints readers with the content and conclusions of important congresses and seminars at home and abroad.

ASSOCIATION NEWS reports on the work of Slovene biology associations.

2. Originality of Articles

Manuscripts submitted for publication in *Acta Biologica Slovenica* should not contain previously published material and should not be under consideration for publication elsewhere.

3. Language

Articles and notes should be submitted in English, or as an exception in Slovene if the topic is very local. As a rule, congress and association news will appear in Slovene.

4. Titles of Articles

Title must be short, informative, and understandable. It must be written in English and in Slovene language. The title should be followed by the name and full address of the authors (and if possible, fax number and/or e-mail address). The affiliation and address of each author should be clearly marked as well as who is the corresponding author.

5. Abstract

The abstract must give concise information about the objective, the methods used, the results obtained, and the conclusions. The suitable length for scientific articles is up to 250 words, and for brief note articles, 100 words. Article must have an abstract in both English and Slovene.

6. Keywords

There should be no more than ten (10) keywords; they must reflect the field of research covered in the article. Authors must add keywords in English to articles written in Slovene.

7. Running title

This is a shorter version of the title that should contain no more than 60 characters with spaces.

8. Introduction

The introduction must refer only to topics presented in the article or brief note.

9. Illustrations and Tables

Articles should not contain more than ten (10) illustrations (graphs, dendrograms, pictures, photos etc.) and tables, and their positions in the article should be clearly indicated. All illustrative material should be provided in electronic form. Tables should be submitted on separate pages (only horizontal lines should be used in tables). Titles of tables and illustrations and their legends should be in both Slovene and English. Tables and illustrations should be cited shortly in the text (Tab. 1 or Tabs. 1-2, Fig. 1 or Figs. 1-2; Tab. 1 and Sl. 1). A full name is used in the legend title (e.g. Figure 1, Table 2 etc.), written bold, followed by a short title of the figure or table, also in bold. Subpanels of a figure have to be unambiguously indicated with capital letters (A, B, …). Explanations associated with subpanels are given alphabetically, each starting with bold capital letter, a hyphen and followed by the text (A - text...).

10. The quality of graphic material

All the figures have to be submitted in the electronic form. The ABS publishes figures either in pure black and white or in halftones. Authors are kindly asked to prepare their figures in the correct form to avoid unnecessary delays in preparation for print, especially due to problems with insufficient contrast and resolution. Clarity and resolution of the information presented in graphical form is the responsibility of the author. Editors reserve the right to reject unclear and poorly readable pictures and graphical depictions. The resolution should be 300 d.p.i. minimum for halftones and 600 d.p.i. for pure black and white. The smallest numbers and lettering on the figure should not be smaller than 8 points (2 mm height). The thickness of lines should not be smaller than 0.5 points. The permitted font families are Times, Times New Roman, Helvetica and Arial, whereby all figures in the same article should have the same font type. The figures should be prepared in TIFF, EPS or PDF format, whereby TIFF (ending *.tif) is the preferred type. When saving figures in TIFF format we recommend the use of LZW or ZIP compression in order to reduce the file sizes. The photographs can be submitted in JPEG format (ending *.jpg) with low compression ratio. Editors reserve the right to reject the photos of poor quality. Before submitting a figure in EPS format make sure first, that all the characters are rendered correctly (e.g. by opening the file first in the programs Ghostview or GSview – depending on the operation system or in Adobe Photoshop). With PDF format make sure that lossless compression (LZW or ZIP) was used in the creation of the *.pdf file (JPEG, the default setting, is not suitable). Figures created in Microsoft Word, Excel, PowerPoint etc. will not be accepted without the conversion into one of the before mentioned formats. The same goes for graphics from other graphical programs (CorelDraw, Adobe Illustrator, etc.). The figures should be prepared in final size, published in the magazine. The dimensions are 12.5 cm maximum width and 19 cm maximum height (width and height of the text on a page).

11. Conclusions

Articles shall end with a summary of the main findings which may be written in point form.

12. Summary

Articles written in Slovene must contain a more extensive English summary. The reverse also applies.

13. Literature

References shall be cited in the text. If a reference work by one author is cited, we write Allan (1995) or (Allan 1995); if a work by two authors is cited, (Trinajstić and Franjić 1994); if a work by three or more authors is cited, (Pullin et al. 1995); and if the reference appears in several works, (Honsig-Erlenburg et al. 1992, Ward 1994a, Allan 1995, Pullin et al. 1995). If several works by the same author published in the same year are cited, the individual works are indicated with the added letters a, b, c, etc.: (Ward 1994a,b). If direct quotations are used, the page numbers should be included: Toman (1992: 5) or (Toman 1992: 5–6).The bibliography shall be arranged in alphabetical order beginning with the surname of the first author, comma, the initials of the name(s) and continued in the same way with the rest of the authors, separated by commas. The names are followed by the year of publication, the title of the article, the full name of the journal (periodical), the volume, the number in parenthesis (optional), and the pages. Example:

Mielke, M.S., Almeida, A.A.F., Gomes, F.P., Aguilar, M.A.G., Mangabeira, P.A.O., 2003. Leaf gas exchange, chlorophyll fluorescence and growth responses of Genipa americana seedlings to soil flooding. Experimental Botany, 50(1), 221–231.

Books, chapters from books, reports, and congress anthologies use the following forms:

Allan, J.D., 1995. Stream Ecology. Structure and Function of Running Waters, 1st ed. Chapman & Hall, London, 388 pp.

Pullin, A.S., McLean, I.F.G., Webb, M.R., 1995. Ecology and Conservation of *Lycaena dispar*: British and European Perspectives. In: Pullin A. S. (ed.): Ecology and Conservation of Butterflies, 1st ed. Chapman & Hall, London, pp. 150-164.

Toman, M.J., 1992. Mikrobiološke značilnosti bioloških čistilnih naprav. Zbornik referatov s posvetovanja DZVS, Gozd Martuljek, pp. 1-7.

14. Format and Form of Articles

The manuscripts should be sent exclusively in electronic form. The format should be Microsoft Word (*.doc) or Rich text format (*.rtf) using Times New Roman 12 font with double spacing, align left only and margins of 3 cm on all sides on A4 pages. Paragraphs should be separated by an empty line. The title and chapters should be written bold in font size 14, also Times New Roman. Possible sub-chapter titles should be written in italic. All scientific names must be properly italicized. Used nomenclature source should be cited in the Methods section. The text and graphic material should be sent to the editor-in-chief as an e-mail attachment. For the purpose of review the main *.doc or *.rtf file should contain figures and tables included (each on its own page). However, when submitting the manuscript the figures also have to be sent as separate attached files in the form described under paragraph 10. All the pages (including tables and figures) have to be numbered. All articles must be proofread for professional and language errors before submission.

A manuscript element checklist (For a manuscript in Slovene language the same checklist is appropriately applied with a mirroring sequence of Slovene and English parts):
English title – (Times New Roman 14, bold)
Slovene title – (Times New Roman 14, bold)

Names of authors with clearly indicated addresses, affiliations and the name of the corresponding author – (Times New Roman 12)
Author(s) address(es) / institutional addresses – (Times New Roman 12)
Fax and/or e-mail of the corresponding author – (Times New Roman 12)
Keywords in English – (Times New Roman 12)
Keywords in Slovene – (Times New Roman 12)
Running title – (Times New Roman 12)
Abstract in English (Times New Roman 12, title – Times New Roman 14 bold)
Abstract in Slovene – (Times New Roman 12, title – Times New Roman 14 bold)

Introduction – (Times New Roman 12, title – Times New Roman 14 bold)
Material and methods – (Times New Roman 12, title – Times New Roman 14 bold)
Results – (Times New Roman 12, title – Times New Roman 14 bold)
Discussion – (Times New Roman 12, title – Times New Roman 14 bold)
Summary in Slovene – (Times New Roman 12, title – Times New Roman 14 bold)
Figure legends; each in English and in Slovene – (Times New Roman 12, title – Times New Roman 14 bold, figure designation and figure title – Times New Roman 12 bold)
Table legends; each in English and in Slovene – (Times New Roman 12, title – Times New Roman 14 bold, table designation and table title – Times New Roman 12 bold)
Acknowledgements – (Times New Roman 12, title – Times New Roman 14 bold)
Literature – (Times New Roman 12, title – Times New Roman 14 bold)
Figures, one per page; figure designation indicated top left – (Times New Roman 12 bold)
Tables, one per page; table designation indicated top left – (Times New Roman 12 bold)
Page numbering – bottom right – (Times New Roman 12)

15. Peer Review

All Scientific Articles shall be subject to peer review by two experts in the field (one Slovene and one foreign) and Brief Note articles by one Slovene expert in the field. With articles written in Slovene and dealing with a very local topic, both reviewers will be Slovene. In the compulsory accompanying letter to the editor the authors must nominate one foreign and one Slovene reviewer. However, the final choice of referees is at the discretion of the Editorial Board. The referees will remain anonymous to the author. The possible outcomes of the review are: 1. Fully acceptable in its present form, 2. Basically acceptable, but requires minor revision, 3. Basically acceptable, but requires important revision, 4. May be acceptable, but only after major revision, 5. Unacceptable in anything like its present form. In the case of marks 3 and 4 the reviewers that have requested revisions have to accept the suitability of the corrections made. In case of rejection the corresponding author will receive a written negative decision of the editor-in-chief. The original material will be erased from the ABS archives and can be returned to the submitting author on special request. After publication the corresponding author will receive the *.pdf version of the paper.

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PREGLEDNA ČLANKA – REVIEW PAPERS:

ČLANKI – ARTICLES:

NOVICE – NEWS: