

Mnogotere vloge silicija izboljšajo uspevanje rastlin

Multiple roles of silicon benefit plants

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Izveček: 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 evlucijski 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 Ls1l 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 rastlinskimi vrstami 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. paradiznik) 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 kutina 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 preklap 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, Henriët 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 privzedom 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 ($\text{SiO}_2 \times n\text{H}_2\text{O}$) (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 vrstke 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 nomenklaturu za standardizacijo poimenovanj vseh različnih oblik fitolitov. Golokhvast in sod. (2014) so našli povezavo med različnimi morfolipii fitolitov in evlucijsko starostjo rastlin. Fitoliti evlucijsko starejših taksonov so v splošnem večji kot pri evlucijsko mlajših taksonih. Poleg tega se pri evlucijsko starejših skupinah pojavlja manj različnih morfolipov 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 izoliral 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 prerezovanje 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. biosilifikacija tesno povezana s polisaharidom kalozo, ki sproži proces biosilifikacije. Pred silifikacijo nastopi še proces lignifikacije (Zhang

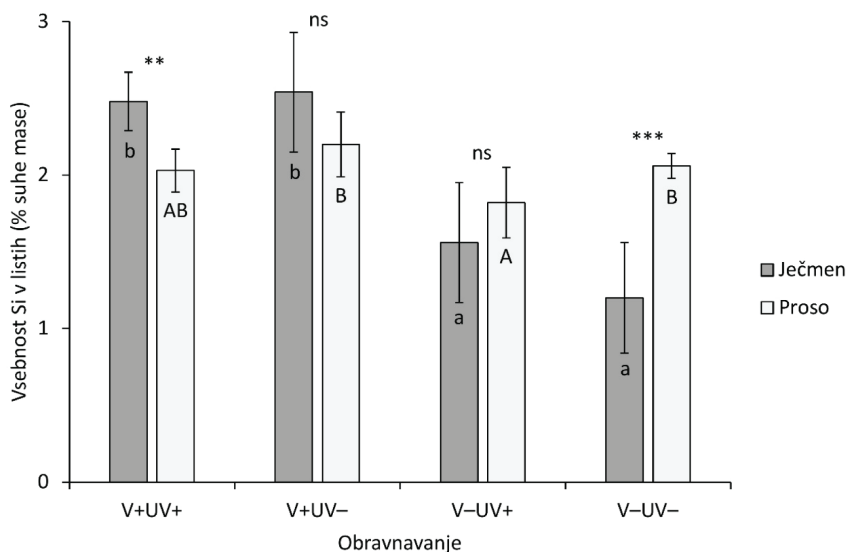
in sod. 2013a). Piperno in sod. (2002) ter Dorweiler in Doebley (1997) so našli neposredno povezavo med ligninom in fitoliti na genetski ravni, saj so ugotovili, da nastanek fitolitov nadzorujejo isti geni kot nalaganje lignina. Si se lahko nalaga tako v koreninah (Parry in Kelso 1975, Sangster 1977, 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 C₃ in C₄ 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).

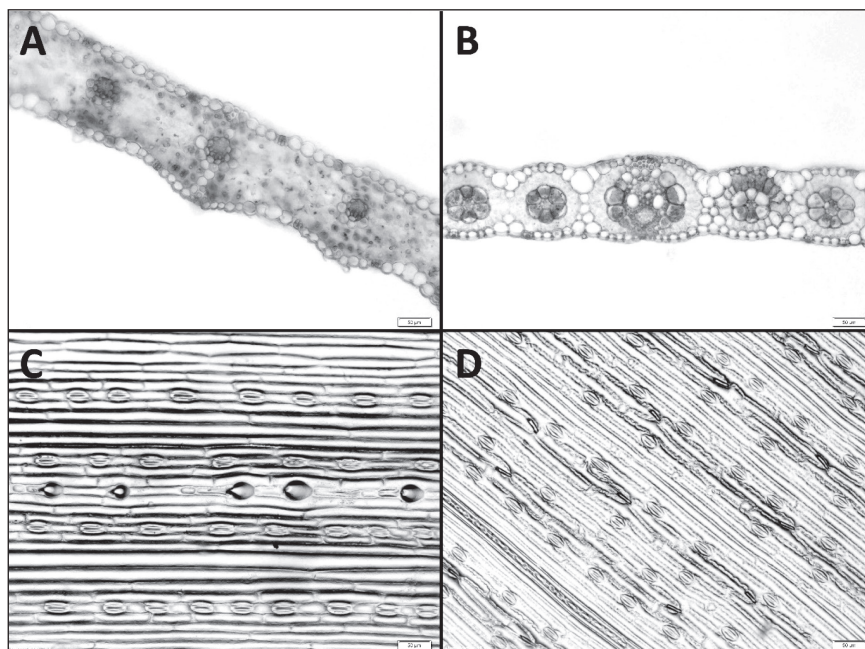
Primerjava vsebnosti Si v listih C_3 vrste, ječmena (Grašič in sod. 2019a), in C_4 vrste, prosa (Grašič in sod. 2019b), pri štirih različnih obravnavanjih (kombinacije zadostne dostopnosti vode in pomanjkanja vode ter naravne ravni UV sevanja in zmanjšane ravni naravnega UV sevanja) pri podobnih okoljskih 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 \pm 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 \pm 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 μ m.

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 μ m.

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 boljшему 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 prerezporejanja 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). Večkratni 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 njihovem 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 abiotске 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 peganje 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 ovojnica (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, zvižanje, otrdevanje, odebelitev, sušenje, povešanje in venenje listov, večjo podvrženost različnim boleznim, motnje pri opravitvi 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 asimilacije CO₂ (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 našteje 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 izboljšanjem 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, Haghghi in Pessaraki 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, Mahdih 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 pregretyh listov preko oddajanja sevanja v srednjevalovnem infrardečem spektru zaradi Si struktura 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 boljše 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 zavirna 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 poveča 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, Poovaiyah 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 Fe²⁺ 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	Vaculik in sod. (2009)
zmanjšana dostopnost v celicah poganjkov preko znižanja koncentracije v simplastu in povišanja v apoplastu	Vaculik in sod. (2012)
povečan razvoj apoplastnih barier in prevodnih tkiv v koreninah	Vaculik 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	Vaculik 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

Arsen (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 tekmovalnosti 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 (Marmioli 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 boleznine 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 našete 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	<i>Magnaporthe grisea</i> (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)
	<i>Cochliobolus miyabeanus</i> (S. Ito & Kurib.) Drechsler ex Dastur	Datnoff in sod. (1991), Winslow (1992), Dallagnol in sod. (2014), Van Bockhaven in sod. (2015)
	<i>Rhizoctonia solani</i> J.G. Kühn	Winslow (1992), Deren in sod. (1994), Rodrigues in sod. (2001, (2003b), Schurt in sod. (2014, 2015)
	<i>Chilo suppressalis</i> Walker	Djamin in Pathak (1967)
	<i>Xanthomonas oryzae</i> (ex Ishiyama) Swings et al. emend. van den Mooter and Swings	Song in sod. (2016)
	<i>Sarocladium attenuatum</i> W. Gams & D. Hawksw.	Winslow (1992)
	<i>Cochliobolus lunatus</i> R.R. Nelson & F.A. Haasis	Winslow (1992)
	<i>Monographella albescens</i> (Thüm.) V.O. Parkinson, Sivan. & C. Booth	Winslow (1992), Tatagiba in sod. (2014)
pšenica	<i>Blumeria graminis</i> (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)
	<i>Phaeosphaeria nodorum</i> (E. Müll.) Hedjar.	Rodgers-Gray in Shaw (2004)
	<i>Mycosphaerella graminicola</i> (Fuckel) J. Schröt.	Rodgers-Gray in Shaw (2004)

Rastlinska vrsta	Patogen	Viri
	<i>Oculimacula yallundae</i> (Wallwork & Spooner) Crous & W. Gams <i>Magnaporthe grisea</i> ¹	Rodgers-Gray in Shaw (2004) 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	<i>Blumeria graminis</i> ²	Carver in sod. (1998)
ječmen	<i>Blumeria graminis</i> ²	Carver in sod. (1987), Wiese in sod. (2005)
proso	<i>Sclerospora graminicola</i> (Sacc.) J. Schröt.	Deepak in sod. (2008), Sapre in sod. (2013)
sirek	<i>Colletotrichum sublineolium</i> Henn. ex Sacc. & Trotter	Resende in sod. (2013)
bananovec	<i>Cylindrocladium spathiphylli</i> Schoult., El-Gholl & Alfieri <i>Fusarium oxysporum</i> Schldtl. <i>Mycosphaerella fijiensis</i> M. Morelet	Vermeire in sod. (2011) Fortunato in sod. (2012, 2014) Kablan in sod. (2012)
oljna palma	<i>Ganoderma boninense</i> Pat.	Najjihah in sod. (2015)
mormodika	<i>Pythium aphanidermatum</i> (Edson) Fitzp. ³	Heine in sod. (2007)
paradižnik	<i>Pythium aphanidermatum</i> ³	Heine in sod. (2007)
krompir	<i>Fusarium sulphureum</i> Schldtl.	Li in sod. (2009)
fižol	<i>Pseudocercospora griseola</i> (Sacc.) Crous & U. Braun <i>Colletotrichum lindemuthianum</i> (Sacc. & Magnus) Briosi & Cavara	Rodrigues in sod. (2010) Polanco in sod. (2013), Antunes da Cruz in sod. (2014), Polanco in sod. (2014), Rodrigues in sod. (2015)
grah	<i>Mycosphaerella pinodes</i> (Berk. & A. Bloxam) Vesterg.	Dann in Muir (2002)
soja	<i>Phakopsora pachyrhizi</i> Syd. & P. Syd. <i>Cercospora sojina</i> Hara	Arsenault-Labrecque in sod. (2012), Antunes Cruz in sod. (2014b) Nascimento in sod. (2014)
kumara	<i>Pythium aphanidermatum</i> ³ <i>Pythium ultimum</i> Trow <i>Cladosporium cucumerinum</i> Ellis & Arthur <i>Sphaerotheca fuliginea</i> (Schldtl.) Pollacci ⁴	Chérif in sod. (1994) Chérif in sod. (1992, 1994) Fawe in sod. (1998) 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	<i>Sphaerotheca fuliginea</i> ⁴ <i>Podosphaera xanthii</i> (Castagne) U. Braun & Shishkoff ⁵ <i>Acidovorax citrulli</i> Schaad et al.	Menzies in sod. (1992) Dallagnol in sod. (2012) Ferreira in sod. (2015)
oljna buča	<i>Podosphaera xanthii</i> ⁵ <i>Erysiphe cichoracearum</i> DC. ⁶ <i>Sphaerotheca fuliginea</i> ⁴	Heckman in sod. (2003), Torlon in sod. (2016) Menzies in sod. (1992) Mohaghegh in sod. (2015)
paprika	<i>Phytophthora capsici</i> Leonian	French-Monar in sod. (2010)
vinska trta	<i>Uncinula necator</i> (Schwein.) Burrill	Bowen in sod. (1992), Reynolds in sod. (1996)
repnjakovec	<i>Erysiphe cichoracearum</i> ⁶	Ghanmi in sod. (2004), Fauteux in sod. (2006), Vivancos in sod. (2015)
kavovec	<i>Hemileia vastatrix</i> Berk. & Broome	Carré-Missio in sod. (2014)
bombaž	<i>Colletotrichum gossypii</i> Southw.	Nogueira de Moura Guerra in sod. (2014)
jagodnjak	<i>Podosphaera aphanis</i> (Wallr.) U. Braun & S. Takam.	Kanto in sod. (2006), Fatema (2014)
češnja	<i>Penicillium expansum</i> Link <i>Monilinia fructicola</i> (G. Winter) Honey	Qin in Tian (2005) Qin in Tian (2005)
vrtnica	<i>Diplocarpon rosae</i> F.A. Wolf <i>Podosphaera pannosa</i> (Wallr.) de Bary	Gillman in sod. (2003) 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 obstutnega 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 energetske 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 trdnjša 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 boljše zaščito pred rastlinojedi nudi v primeru nevretenčarjev kot v primeru vretenčarjev (Vicari in Bazely 1993). Tudi novejša in bolj evolucijsko obarvana raziskava se nagibajo k dejstvu, da Si nima tako odločilne vloge pri odvratanju 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 našete 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	<i>Cnaphalocrocis medinalis</i> Guenée (Insecta, Lepidoptera)	Ye in sod. (2013), Han in sod. (2016)
	<i>Scirpophaga incertulas</i> Walker (Insecta, Lepidoptera)	Ranganathan in sod. (2006), Jeer in sod. (2016)
	<i>Sogatella furcifera</i> Horvath (Insecta, Hemiptera)	Salim in Saxena (1991)
	<i>Agriolimax reticulatus</i> Müller (Mollusca, Gastropoda)	Wadham in Parry (1981)
	<i>Nilaparvata lugens</i> Stål (Insecta, Hemiptera)	He in sod. (2015)
pšenica	<i>Schizaphis graminum</i> Rondani (Insecta, Hemiptera, Aphididae)	Basagli in sod. (2003), Moraes in sod. (2004), Gomes in sod. (2005), Goussain in sod. (2005)
	<i>Oryctolagus cuniculus</i> Linnaeus (Mammalia, Leporidae)	Cotterill in sod. (2007)
koruza	<i>Ostrinia nubilalis</i> Hübner (Insecta, Lepidoptera)	Coors (1987)
sladkorni trs	<i>Eldana saccharina</i> Walker (Insecta, Lepidoptera)	Kvedaras in sod. (2005, 2007a,b)
	<i>Diatraea saccharalis</i> Fabricius (Insecta, Lepidoptera)	Sartori de Camargo in sod. (2014)
stoklasa	<i>Microtus ochrogaster</i> Wagner (Mammalia, Cricetidae)	Gali-Muhtasib in sod. (1992)
ljuljka	<i>Schistocerca gregaria</i> Forsskål (Insecta, Orthoptera) ¹	Massey in sod. (2007), Hunt in sod. (2008), Garbuzov in sod. (2011)
	<i>Microtus agrestis</i> Linnaeus (Mammalia, Cricetidae) ²	Massey in Hartley (2006), Massey in sod. (2007)
	<i>Oscinella frit</i> Linnaeus (Insecta, Diptera)	Moore (1984)
	<i>Spodoptera exempta</i> Walker (Insecta, Lepidoptera) ³	Massey in Hartley (2009)
bilnica	<i>Schistocerca gregaria</i> (Insecta, Orthoptera) ¹	Massey in sod. (2007), Hunt in sod. (2008)
	<i>Microtus agrestis</i> (Mammalia, Cricetidae) ²	Massey in Hartley (2006), Massey in sod. (2007)
	<i>Spodoptera exempta</i> (Insecta, Lepidoptera) ³	Massey in Hartley (2009)
masnica	<i>Microtus agrestis</i> (Mammalia, Cricetidae) ²	Massey in sod. (2008)
	<i>Spodoptera exempta</i> (Insecta, Lepidoptera) ³	Massey in Hartley (2009)
kumara	<i>Bemisia tabaci</i> Gennadius (Insecta, Hemiptera)	Correa in sod. (2005)
krizantema	<i>Macrosiphoniella sanborni</i> Gillette (Arthropoda, Hemiptera, Aphididae)	Jeong in sod. (2012)
kavovec	<i>Meloidogyne exigua</i> 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 jeklnar, 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-SiO₂ (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 abiotiski 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.

Viri

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