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Title:
The controversies of silicon’s role in plant biology

Date:
2019-01-01

Citation:
Kronzucker, H. (2019). The controversies of silicon’s role in plant biology. New Phytologist, 221 (1), pp.67-85. https://doi.org/10.1111/nph.15343.

Persistent Link:
https://hdl.handle.net/11343/284158

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Article type : TR - Commissioned Material - Tansley Review

Tansley review

The controversies of silicon's role in plant biology

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Received: *20 April 2018*
Accepted: *5 June 2018*

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Summary

Silicon (Si) is not classified as an essential plant nutrient, and yet, numerous reports have shown its beneficial effects in a variety of species and environmental circumstances. This has created much confusion in the scientific community with respect to its biological roles. Here, we link molecular and phenotypic data to better classify Si transport, and critically summarize the current state of understanding of the roles of Si in higher plants. We argue that much of the empirical evidence, particularly that derived from recent functional genomics, is at odds with many of the mechanistic assertions surrounding silicon's role. In essence, these data do not support reports that Si affects a wide range of molecular-genetic, biochemical, and physiological processes. A major reinterpretation of silicon's role is therefore needed, which is critical to guide future studies and inform agricultural practice. We propose a working model, which we term the 'apoplastic obstruction hypothesis', that attempts to unify the various observations on silicon's beneficial influences on plant growth and yield. This model argues for a fundamental role of Si

as an extracellular prophylactic agent against biotic and abiotic stresses (as opposed to an active cellular agent), with important cascading effects on plant form and function.

Key words: abiotic stress, apoplast, biotic stress, membrane transport, plant nutrition, silicon (Si).

I. Introduction

Nearly 25 years ago, the seminal review by Epstein (1994), 'The anomaly of silicon in plant biology', became a turning point of accelerated interest in silicon's properties and benefits to plants. Before that, the bulk of research efforts and discoveries had been pioneered by Japanese scientists whose reports, originally published in Japanese, were summarized by Ma *et al.* (2001). Apart from these major works, there is a dearth of research in the peer-reviewed literature before 1994, with *c*. 200 papers dealing with silicon (Si) effects in plants, as opposed to the *c*. 800 articles focusing on various aspects of silicon's potential in plants that have been published since (Fig. 1). As a result, many important discoveries, such as the identification of Si transporters, have impacted our understanding of Si in plants, and mounting evidence supporting the advantages of Si fertilization has finally, in 2015, led the International Plant Nutrition Institute (IPNI) to upgrade Si from complete omission to the status of 'beneficial substance' (www.ipni.net/nutrifacts).

The chemistry of Si is complex and difficult to master even in simple laboratory practice (Iler, 1979; Evered & O'Connor, 1986; Voogt & Sonneveld, 2001), and many features intrinsic to Si have hampered its widespread application in agriculture. For one, the silicate salts typically used to supply Si in growth media (e.g. potassium silicate and sodium silicate) are highly alkaline and can cause precipitation issues if not carefully handled (Voogt & Sonneveld, 2001). Moreover, orthosilicic acid ($Si(OH)_4$; $pK_{a1} = 9.84$, $pK_{a2} = 13.2$, at 25 °C), the form of Si accessible to plants (Casey *et al.*, 2004), is soluble in water only up to *c*. 2 mM at 25 °C, above which polymerization into silica (SiO_2) gel begins to occur (Ma *et al.*, 2001). From a biochemical perspective, $Si(OH)_4$ is largely uncharged and unreactive at physiological pH. As Pace (2001) notes, unlike carbon (C), Si cannot engage in as many chemical bonds with as many other atoms, and is thus largely 'monotonous' (forming mostly silicates and SiO_2 polymers), compared to the vast combinations of organic macromolecules. As a result, in spite of the impressive body of Si research now in the literature, the precise role of Si in plants remains largely unknown, and in particular the potential for its practical application largely unexploited.

In essence, there are four main areas of contention surrounding Si in higher plants: (1) its absorption (or lack thereof), (2) its essentiality, (3) its nutritional role (i.e. as a fertilizer), and (4) the mechanism(s) by which it confers protections against biotic and abiotic stresses.

One of the most puzzling properties of Si is its differential absorption by plants. Depending on the plant species, soil properties, Si source, and Si amount, *in-planta* Si contents can vary from 0.1% (near the detection limit) to 10% (on a dry-weight basis; Epstein, 1994). This gives rise to additional confusion, since the beneficial properties of Si are generally linked to the amount absorbed by the plant (Ma, 2004). Consequently, some plant species benefit minimally from Si fertilization compared to others, a distinction that is often overlooked in experiments, which can lead to faulty conclusions and unrealistic expectations. Previous studies have attempted to phenotype and classify plants according to their ability to absorb Si (Hodson *et al.*, 2005; Trembath-Reichert *et al.*, 2015), a difficult endeavor considering the numerous factors that can influence the data. With novel experimental techniques, the advancement of genomics, and developments such as the discovery of Si transporters, new opportunities are available to characterize accumulator and non-accumulator plants on the basis of specific molecular features (Section II).

The essentiality of Si for plants has been the subject of much debate and many reviews (Epstein, 1994, 1999, 2009; Datnoff *et al.*, 2001; Y. Liang *et al.*, 2015), and will not be revisited in detail here. Since the pioneering works of Sprengel and von Liebig in the early- to mid-1800s (van der Ploeg *et al.*, 1999), and the refinements by Arnon and Stout (1939), plant nutritionists have maintained the exclusion of Si from the list of essential mineral elements for higher plants (i.e. with the exception of horsetail (*Equisetum arvense*); Gregoire *et al.*, 2012; Vivancos *et al.*, 2016). Epstein (1994, 2001) argued that the essentiality of Si is experimentally challenging to assess since Si is one of the most abundant elements in Earth’s crust and a ubiquitous contaminant, and thus difficult to exclude from plant growth media entirely. Cognizant of this reality, our review will specifically focus on the tangible, measurable benefits associated with Si amendment in excess of the background contamination found in various growth media, both natural and artificial.

Considering that plants cannot grow in an environment completely devoid of Si, the more realistically important question is whether plants will benefit from Si through addition to experimental growth solutions or soil fertilization. A few reports have claimed that Si fertilization can enhance plant growth and yield, while others have refuted such claims. This review will cast a critical eye on the wide-ranging results in the literature on Si effects, in an effort to bring consensus to the debate (Section III).

One area of Si biology that is settled involves the alleviation of stress (e.g. the decreases in growth rate; Grime, 2001), both biotic and abiotic (Sections IV and V, respectively), and numerous studies over the years have attempted to decipher the mechanisms by which Si confers such protection. These efforts have proven challenging on many levels, however, perhaps most fundamentally because of the discrepancy between the view of $Si(OH)_4$ as a biochemically inert substance and the numerous and wide-ranging mechanistic assertions (e.g. genetic, biochemical, and physiological) put forth in the literature. It is our opinion that it is highly improbable that Si is as biologically versatile, and, consequently, its protective role, regardless of the stress, more likely stems from a common mechanism. Through comparative analysis of the literature describing silicon's alleviation of different stresses, both biotic (e.g. microbial pathogens, herbivorous arthropods) and abiotic (e.g. salinity, heavy metal, nutrient deficiency), we propose a working model of silicon's role in higher plants, termed the 'apoplastic obstruction hypothesis' (Section VI).

II. Silicon transport in plants: to absorb or not to absorb

Plants will absorb Si in the form of $Si(OH)_4$ from soil or nutrient solutions. The maximum solubility of $Si(OH)_4$ in solution is *c*. 2 mM, and its concentration in soil solutions usually varies between 0.1 and 0.6 mM (Raven, 1983; Epstein, 1994). Under similar conditions, plant species have different abilities to accumulate Si, a reality that has been known, if poorly understood, for a long time.

Handreck and Jones (1967) proposed a classification of plant species based on their Si content and identified three groups: low, intermediate, and high accumulators. At the time, however, this classification could not take into account the fact that specific biological mechanisms could explain the inter-species variation. Years later, Takahashi *et al.* (1990) refined the classification system by categorizing plants based on basic mechanistic understandings of Si uptake. The authors described three mechanisms, active, passive, and rejective, that associate, quite closely, with the high-, intermediate-, and low-accumulator plants, respectively. Active accumulators have a shoot Si content ranging from 1.5 to 10% and include monocots such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), and sorghum (*Sorghum bicolor*). The passive accumulators encompass mostly dryland Gramineae with a shoot Si content of 0.5–1.5%. Finally, the rejective classification applies to plants with Si content of <0.2%, and, at the time, was associated with most dicots.

With more data available on Si content in plants, Hodson *et al.* (2005) conducted an exhaustive analysis of 735 plant species from 125 studies and normalized the data based on measurements from at least two independent studies for each species, in order to classify plants on their ability to accumulate Si. At a time when Si transporters had not been identified, this dataset provided a valuable resource on the phylogenetic distribution of Si content in the plant kingdom.

Classifications aside, the mechanisms by which plants absorb Si had long been elusive. Transpiration was believed to be one of the main factors determining Si uptake in plants. While translocation of $Si(OH)_4$ from the xylem to the aerial part of the plant is certainly facilitated by transpiration, the idea that this process alone dictates the amount of Si found in a plant has been shown to be erroneous. Ma *et al.* (2001) first showed that transpiration had little influence on the Si content in rice plants. Additionally, transpiration alone could not explain the wide variation in Si content observed among plants by Bélanger *et al.* (2016), who offered evidence that much of the variation in Si content could be explained by Si transport in roots. By using soybean (*Glycine max*) cultivars that differed markedly in their ability to absorb Si, the authors grafted interchangeably the rootstock of one cultivar with the scion of another, and supplied the plants with Si. Their results showed that the Si content found in leaves was directly associated with the rootstock while the measures of evapotranspiration between the plants remained unchanged (Fig. 2). This provided strong evidence that the mechanisms influencing Si uptake were inherent to the roots.

The seminal discoveries of Si transporters in rice roots by Ma *et al.* (2006, 2007) have laid the foundation for our understanding of how plants can accumulate the element, and which plants do so. At the same time, these findings offer the opportunity to classify plants on the basis of precisely defined molecular mechanisms rather than solely on empirical observations. In essence, Si enters the plant from the external environment in the form of $Si(OH)_4$ through specific influx channels (termed Lsi1), while efflux transporters (termed Lsi2) mediate the loading of Si into the xylem and thus facilitate root-to-shoot translocation, which, in turn, moves Si to the aerial parts of the plant where it deposits as amorphous SiO_2 (for review, see Ma & Yamaji, 2015).

Lsi1, providing primary entry of $Si(OH)_4$ into plant root cells (and to a lesser extent, arsenious acid ($As(OH)_3$) and boric acid ($B(OH)_3$); Mitani-Ueno *et al.*, 2011), belongs to the superfamily of major intrinsic proteins (MIPs, also known as aquaporins (AQPs); Ma *et al.*, 2006). AQPs are a class of channel-forming proteins that facilitate the transport of water and many other small solutes across cell membranes. They have a characteristic hourglass-like structure made up of six transmembrane (TM) domains, and two half TM helices protruding from opposite sides towards the center of the pore (Murata *et al.*, 2000). The two half TM helices form a constriction hosting two NPA (asparagine-proline-alanine) domains. The pore forms another constriction, often referred to as the selectivity filter, and is composed of four amino acids (AAs). The AAs at the selectivity filter are usually highly conserved and involved in the solute specificity of a given AQP (Hove & Bhave, 2011). Interestingly, the phylogenetic distribution of all known Si-influx transporters identified in crops, including monocots and dicots, showed a specific clustering within the Nodulin 26-like intrinsic protein III (NIP-III) subgroup of AQPs. Moreover, these transporters have a selectivity filter composed of a conserved GSGR (glycine-serine-glycine-arginine) motif. In a recent study, Deshmukh *et al.* (2015) were able to further establish that the distance between the NPA domains was another selective feature for Si transport. They showed that, among other plants, tomato was a poor Si accumulator because it contained 109 AAs between the NPA domains, instead of the conserved 108 AAs among high accumulators. Therefore, plant AQPs belonging to the NIP-III subgroup with a GSGR selectivity filter and two NPA domains separated by 108 AAs can be categorized as being permeable to $Si(OH)_4$ (Fig. 3).

On the basis of the precise molecular characteristics conferring Si permeability to certain AQPs (Mitani & Ma, 2005; Ma *et al.*, 2006; Deshmukh *et al.*, 2015), and of the direct association established between a plant's ability to absorb Si and the presence of those AQPs, we suggest that molecular criteria should be adopted to classify plants for Si uptake. As such, plants could be categorized as accumulators or non-accumulators as per the presence of NIP-III channels possessing the necessary features for Si permeability (Fig. 3). With the availability of genomic data increasing daily, one could, in essence, predict whether a plant can absorb Si or not by simply aligning sequences indicative of functional NIP-IIIs. Among accumulators, quantitative differences remain a fascinating subject and might be explained by agronomic traits such as root architecture, presence of leaf silica cells (Kumar *et al.*, 2017b), leaf size and development (e.g. as is the case with strawberry (*Fragaria* × *ananassa*); Ouellette *et al.*, 2017), growth conditions particularly with respect to the rooting media (e.g. soil properties, hydroponics, pH, plant-available Si), or the functionality of downstream Si transporters such as Lsi2 (Mitani *et al.*, 2009) or shoot (node)-localized Lsi3 and Lsi6 (Ma & Yamaji, 2015; Yamaji *et al.*, 2015).

Although understanding of Si transport has come a long way, there remains much to investigate. Regarding Lsi2, the fundamental issue of the mechanism of transport remains obscure. It is held that Lsi2 belongs to a class of putative anion transporters, showing similarity with the arsenite efflux transporter ArsB from bacteria and Archaea, and functions as a $Si(OH)_4/H^+$ antiporter (Ma *et al.*, 2007). However, direct evidence for this transport process is currently lacking. If such a mechanism exists, experimental methods that elucidated the mechanism of transporters like NHX1 and SOS1 (Na^+/H^+ antiporters; Apse *et al.*, 1999; Qiu *et al.*, 2002), should, hypothetically, shed light on Lsi2 functionality. The mechanism of Si deposition and accumulation is also unclear but has recently garnered increased attention (Exley, 2015; Guerriero *et al.*, 2016; Kumar *et al.*, 2017b). Once the solubility of $Si(OH)_4$ is exceeded (i.e. >2 mM), SiO_2 polymerization occurs, and, for cells, this can be toxic (Iler, 1979; see also Montpetit *et al.*, 2012; Exley, 2015); thus, it stands to reason that $Si(OH)_4$ transported through healthy root cells (via Lsi1 and Lsi2) must maintain a cytosolic concentration <2 mM, although direct cytosolic measurements are currently lacking. The majority of Si is found polymerized in the apoplast (e.g. around exodermal and endodermal root cells and leaf epidermal cells; Sangster *et al.*, 2001; Gong *et al.*, 2006), and cell-wall constituents such as (hemi)cellulose, callose, pectin, and lignin have been demonstrated to interact with $Si(OH)_4$ as ‘templates’ or ‘scaffolding’ for silicification (Guerriero *et al.*, 2016, and references therein). Si can also polymerize in specialized cells and cellular structures of some species (particularly grasses), such as leaf silica and long cells, and spikelet hairs and papillae (Rafi *et al.*, 1997), and interesting preliminary evidence for biological control of this process has emerged (Kumar *et al.*, 2017a; Kumar *et al.*, 2017b; Kumar & Elbaum, 2018).

III. The role of silicon in plants: not just a matter of semantics

Although there is no doubt that Si can be beneficial in protecting plants against stress, both biotic and abiotic (see Sections IV and V, respectively), the mechanistic underpinnings of such protections remain elusive. More fundamentally, however, the question of silicon's role in the absence of stress remains a contentious issue, as some studies have reported growth- and yield-promoting effects under such conditions, in contradiction with other reports (Table 1). It is important to reiterate, though, that Si is not an essential element for higher plants (see Section I), failing to fulfill the criteria laid out by Arnon and Stout (1939), namely: (1) deficiency in the element makes it impossible for the plant to complete its life cycle, (2) deficiency symptoms are specific to the element in question and can only be corrected by supplying the element, and (3) the element is directly involved in the nutrition of the plant and not merely correcting some unfavourable condition of the growth regime. Here, we make the case that it is specifically the third criterion that is confounding much of the research on Si, that is, there is a conflation of Si-induced alleviation of stress with the postulate of a nutritional role in plants. As we shall see, the preponderance of the evidence suggests that Si *per se* does not promote plant growth, function, or metabolic activity, but rather prevents or mitigates the strains imposed by stress, and this, ultimately, is reflected in improvements in plant growth, function, and metabolic activity. We believe this is an important distinction to make, and not just a matter of semantics.

At the physiological level, most studies suggest that, in the absence of stress, Si supplementation has little or no effect. For instance, Ma *et al*. (2002) were among the first to compare the photosynthetic activity of rice plants with and without Si supplementation and could not find any differences. As Table 1 shows, the majority of studies demonstrate no effect of Si on measures such as biomass, enzyme activity, membrane potential, ion and water transport, respiration, and photosynthesis. By contrast, Si effects are quite generalized under conditions of stress, and, importantly, such effects often return physiological measures back to control levels, rather than surpassing baseline (Fig. 4a).

The advent of 'omics' technologies has offered the opportunity to investigate with unprecedented precision how Si supplementation affects a plant. Watanabe *et al.* (2004) first demonstrated that Si supplementation had essentially no effects on gene expression in rice, with only one out of *c.* 9000 genes analyzed being significantly altered in its expression. Similarly, a proteomic analysis by Nwugo and Huerta (2011) showed Si supplementation in rice resulted in statistically significant changes in the abundance of only four proteins, and another study with rice could not identify distinct metabolic pathways influenced by Si in control plants (Brunings *et al.*, 2009). Fauteux *et al.* (2006) reported the first complete transcriptomic analysis of a plant under Si supply and demonstrated that Si had no significant effect on the expression of any but two of the *c.* 28500 genes analyzed in Arabidopsis (*Arabidopsis thaliana*). In wheat, Chain *et al.* (2009) observed that, of the *c.* 55000 transcripts analyzed, only 47 were significantly altered by Si supplementation and most were downregulated stress-related genes. Interestingly, in pathogen-inoculated plants, >3000 genes were differentially expressed and the authors observed a nearly perfect reversal in the transcript profile when Si was supplied, suggesting that rather than directly being involved in regulating gene expression, Si prevented or attenuated the effects on transcription imposed by the stress. More recently, an analysis of soybean showed Si supplementation had no effect on gene expression related to any distinct metabolic pathway, with only 50 genes altered (falling into categories of stress-related or 'hypothetical protein') out of *c.* 55000 analyzed under control conditions (Rasoolizadeh *et al.*, 2018). Similar to the case with wheat, the differentially expressed genes (DEGs) in response to a pathogen challenge (*c.* 3000) reverted to a pattern of expression observed in non-stressed plants when Si supplementation occurred, once again supporting the notion that Si did not alter gene expression *per se*, but rather interfered with strains (leading to gene-expression alterations) induced by stress (Fig. 4b). Interestingly, if transcriptomic studies showed little/no effect of Si on gene expression in control plants, similar analyses with essential elements yielded much larger effects. For example, the response to a 24-h deficiency in nitrogen (N), phosphorus (P), and potassium (K) resulted in 1946, 382, and 814 DEGs (out of *c.* 27,000 loci analyzed), respectively, in rice (Takehisa *et al.*, 2013). Taken together, these results reinforce the concept that Si has a very limited direct role on unstressed plants.

Although the majority of the studies we surveyed demonstrated a lack of a Si effect under stress-free conditions, there were some exceptions (Table 1). For example, Gong *et al.* (2006) and Flam-Shepherd *et al.* (2018) did observe statistically significant gains in biomass with Si supplementation when NaCl supply was minimal in hydroponically-grown rice seedlings. It was clear, however, that the beneficial effects of Si were maximal when salt stress was highest. Detmann *et al*. (2012) observed many benefits with Si supplementation in mature rice, including increases in crop yield, CO_2 assimilation, and mesophyll conductance, in contradiction to other studies with rice (Table 1). It is unknown whether the fluctuating environmental conditions over the *c*. 90-d experimental period, coupled with the apparent lack of aeration of the nutrient solution, imposed unintended stresses on the plants. In transcriptomic analyses, only Van Bockhaven *et al*. (2015) claimed a large effect of Si on gene expression in stress-free rice in stark contrast with previous studies (Watanabe *et al*., 2004; Fauteux *et al*., 2006; Brunings *et al*., 2009; Chain *et al*., 2009; Rasoolizadeh *et al*., 2018 ; J. F. Ma *et al*., unpublished). Surprisingly, the number of DEGs reported (nearly 2,000) even exceeds that found elsewhere under stress (e.g. Brunings *et al*., 2009), suggesting an influence of unaccounted stress under their experimental conditions. Nevertheless, taken as a whole, the results indicate that there is no reproducible systemic change nor are there cascading effects (e.g. with genes part of clear metabolic or signaling pathways) associated with Si fertilization.

IV. Silicon and biotic stress: beyond mechanical barriers and defence priming

While the benefits of Si fertilization on unstressed plants remain contentious, the same cannot be said for the expanding evidence supporting the positive role of Si in stressed plants. The initial theory concerning the mode of action of Si in plant prophylaxis involved the establishment of a mechanical barrier impeding fungal progress. This stemmed from Wagner (1940), who showed that Si offers protection against powdery mildew (*Sphaerotheca fuliginea*) on different host plants and was the first to suggest that the increased silicification of the host cell wall prevented penetration of the pathogen. This work laid the foundation for the mechanical-barrier hypothesis that is still being conveyed to this day, despite the fact that, as early as 1965, Okuda and Takahashi (1965), citing Yoshi (1941), who measured leaf toughness, reported: ‘From this result, it seemed that Si protected the rice plant against blast disease, but the increase in mechanical toughness of the plant tissue resulting from absorbed Si is not sufficient to explain the mechanism of protection’. Indeed, no observations have directly linked cell-wall reinforcement with penetration failure by the fungus.

The possibility that Si played a role other than a mechanical barrier in the resistance process was first suggested by Samuels *et al.* (1991) and Chérif *et al.* (1992), who observed that plants reacted more promptly to infection by accumulating phenolic-like material that hindered the propagation of the parasite. Corroborating evidence that Si played more than a mechanical-barrier role *in planta* was provided when the interaction between cucumber (*Cucumis sativus*) and powdery mildew was further analyzed at the chemical level (Fawe *et al.*, 1998). The authors detected and identified flavonoids and phenolic acids that were specifically and strongly induced in a pattern typical of phytoalexins, as a result of Si treatment. Thus, Si was hypothesized to play an active role in disease resistance by stimulating defence mechanisms. Subsequently, through electron microscopy studies and chemical analyses of rice, Rodrigues *et al.* (2003, 2004) showed that plants treated with Si fended off rice-blast infection through production of electron-dense material composed of momilactones, which act as phytoalexins in rice. At the same time, similar results were obtained for wheat-powdery mildew interactions on plants supplied with Si (Bélanger *et al.*, 2003; Rémus-Borel *et al.*, 2009). Thereafter, numerous papers have associated the prophylactic role of Si against diseases with some form of defence response by the plant (Y. Liang *et al.*, 2015, and references therein).

For the most part, studies that have shown heightened defence responses in the presence of Si have speculated on the role of Si in the process. Hypotheses that soluble Si can act as a secondary messenger, a modulator of defence responses, or a priming agent (Fawe *et al.*, 2001; Fauteux *et al.*, 2005; Van Bockhaven *et al.*, 2013) have never been fully tested in the presence of a proper genetic model, until recently. Indeed, by exploiting Arabidopsis mutants able to absorb larger quantities of Si, but deficient in the activation of the salicylic-acid (SA) pathway, Vivancos *et al.* (2015) directly tested if the protective effect of Si became null or significantly altered, given the presumed inability of the plant to mount defence reactions against powdery mildews. It was quite surprising to observe that plants transformed for high Si absorption and supplied with Si displayed resistant phenotypes in spite of having lost the ability to produce defence reactions involving the SA pathway. This meant that Si, in the form of $Si(OH)_4$, did not replace SA as a surrogate secondary messenger in the induction of defence reactions, as previously proposed (Fawe *et al.*, 2001). These observations strongly suggest that other factors are at play in the Si-mediated protection of plants against fungal diseases.

If the above results appear conflicting at first, they open the way to an alternative hypothesis that would unify the modes of action behind the observed phenomena. The prophylactic role of Si is overwhelmingly associated with pathogens that have a biotrophic phase (e.g. powdery mildews, oomycetes, and rice blast; Table 2). For instance, powdery mildews (strict biotrophs), are particularly well controlled by Si. Among hemibiotrophs, rice blast, caused by the fungus *Magnaporthe grisea*, is arguably the most commonly reported disease to be controlled by Si. As such, the suggestion that Si can confer 'broad-spectrum disease resistance' (Van Bockhaven *et al.*, 2013), notwithstanding the fact that it does not apply to non-accumulator species, ignores the overwhelming evidence of field and experimental data associating the benefits primarily against biotrophic and hemibiotrophic pathogens and overlooks the negative reports with necrotrophs. For instance, Rodgers-Gray & Shaw (2004) could not observe any effects against *Fusarium culmorum*, while reporting protection against powdery mildew on wheat. Other necrotrophs, such as *Cercospora sojina*, *Pythium aphanidermatum*, *Bipolaris oryzae*, and *Sclerotinia homeocarpa* have been reported to be unaffected by Si treatment (Malvick & Percich, 1993; Rodgers-Gray & Shaw, 2004; Heine *et al.*, 2006; Nascimento *et al.*, 2014). Also, the literature is obviously biased against reporting negative results, and our own experience has shown repeatedly that Si had no effect against typical necrotrophs such as *Botrytis cinerea* and *Sclerotinia sclerotiorum*. *Bipolaris oryzae* remains an interesting intermediate model, because it is among the pathogens controlled by Si, albeit with less frequency and efficiency than *M. grisea*, and, while being considered a necrotroph, it produces host-selective toxins and its genome codes for effector proteins, features not typically observed for necrotrophs (Condon *et al.*, 2013). In the last few years, the annotation of plant pathogen genomes has highlighted the presence and importance of effector proteins, most notably in the case of biotrophs and hemibiotrophs, in a compatible host-pathogen interaction. Effectors modify host cell structure, metabolism, and function, and interfere with the signaling pathways required for host invasion or triggering host resistance (Giraldo & Valent, 2013). Fungal effectors are first released into the apoplast and can be translocated into the cytoplasm through the cell membrane or the extrahaustorial matrix (EHM) (Bozkurt *et al.*, 2012). Interestingly, SiO_2 deposition in plants is frequently located in the apoplast and, more precisely, at the interface of the plasma membrane with the cell wall (Bauer *et al.*, 2011; Zhang *et al.*, 2013). In a recent review, Wang and Wang (2018) highlighted how the apoplast is a site of intense interactions of many effectors with plant targets. Indeed, the appressorium and the haustorium of powdery-mildew fungi are structures of active release of effectors (Giraldo & Valent, 2013): the appressorium releases effectors into the apoplast to prevent the action of plant proteases, and the haustorium releases effectors into the cytoplasm through the EHM to alter plant defences. Given that the apoplast and the EHM are within the confines of Si deposition (Ghanmi *et al.*, 2004), and, based on our observations, it seems not only plausible but logical that Si could interfere with effectors reaching their targets or plant signals being recognized by the pathogen. This would prevent the invading fungus from inhibiting plant defences, which results in the expression of the complete array of defence mechanisms, or alternatively from recognizing the plant as a compatible host (Holub & Cooper, 2004; Nuernberger & Lipka, 2005). Considering the superior prophylactic role of Si against biotrophs, the heavy reliance of biotrophs on effectors to maintain their virulence, and the site of Si deposition coinciding with effector release, a link between Si and effectors is strongly supported.

In an effort to test this hypothesis, Rasoolizadeh *et al*. (2018) looked at the expression of effectors of the hemibiotroph *Phytophthora sojae* and defence reactions of soybean plants grown in the absence and presence of Si. Their data clearly show a protective effect of Si in soybean, accompanied by a significant reduction of effector expression in Si-supplied plants during the biotrophic phase of *P. sojae*, together with a similarly reduced expression of plant receptors. The results support the concept that Si interferes with effector-receptor expression, which, in turn, confers resistance to the plant. As the role and localization of effectors released by plant pathogens become better defined, it should become possible to investigate mechanistically if and how Si interacts with them and affects their compatibility with the plant.

Research on Si-induced protections against herbivorous insects has followed a similar trajectory to that of fungal pathogens. For example, improved plant defence against arthropods under Si supplementation has also long suggested a mechanical form of protection (Reynolds *et al.*, 2009, 2016). As early as 1955, the reduction of damage to rice plants by the chewing herbivore *Chilo simplex* was postulated to be due to increased strength of the rice stem following Si accumulation (Sasamoto, 1955). More recently, a study of another chewing herbivore *Spodoptera exempta* directly showed that Si acts as a physical defence for three grasses, increasing the abrasiveness of the leaves, and leading to increased wear of mandibles (Massey & Hartley 2009; cf Kvedaras & Keeping, 2007).

Also in line with fungal studies (Fauteux *et al*., 2005), molecular-based defences of Si-treated plants against insects (in particular piercing-sucking types) have been proposed (Gomes *et al.*, 2005). Goussain *et al.* (2005) showed that stylet penetration of wheat aphid (*Schizaphis* *graminum*) was not impeded by Si in wheat plants; however, the stylet was withdrawn more often, resulting in a reduction of probing time, leading the authors to conclude that chemical changes due to Si absorption by the plant were likely responsible. Recently, a study in rice suggested that Si provision led to a higher level of jasmonate-mediated defences against the rice leaffolder, *Cnaphalocrocis medinalis* (Ye *et al.*, 2013).

It has been proposed that plant-insect interactions involve a multi-layered plant defence response mediated by herbivory-associated molecular pattern (HAMP)- and effector-triggered immunity (Hogenhout & Bos, 2011). Insect (Hemipteran) effectors are reportedly recognized by similar classes of immune receptors as those by pathogen virulence effectors (Smith & Clement, 2012; Kaloshian & Walling, 2016a). This is in line with predictions that phloem-feeding insects cause only minor tissue damage and induce defence-signalling pathways resembling those activated against biotrophic and hemibiotrophic pathogens (Walling, 2001; Kusnierczyk *et al.*, 2007). Recent evidence indicates that herbivore-associated endosymbionts (Wang *et al.*, 2017) and the constituents of oral secretions, saliva, eggs (i.e. oviposition fluids), and frass, notably effectors, play an important role in manipulating direct and indirect plant defences (Hilfiker *et al.*, 2014), dramatically reshaping plant transcriptomes, proteomes, and metabolomes (Wu & Baldwin, 2010). Insect effectors have been identified across a range of species, feeding guilds, and for both specialists and generalists, including the Hessian fly (*Mayetiola destructor*; Zhao *et al.*, 2015), brown planthopper (*Nilaparvata lugens*; Ji *et al.*, 2017), tobacco hawk moth (*Manducta sexta*; Halitschke *et al.*, 2001), corn earworm (*Helicoverpa zea*; Musser *et al.*, 2012), cricket (*Teleogryllus taiwanemma*; Yoshinaga *et al.*, 2007), vinegar fly (*Drosophila melanogaster*; Yoshinaga *et al.*, 2007), and several aphid species, including pea aphid (*Acyrthosiphon pisum*; Carolan *et al.*, 2011) and green peach aphid (*Myzus persicae*; Mugford *et al.*, 2016). As these herbivore-associated effectors are derived from the insect or its microbial inhabitants, they are expected to be diverse in structure, function, and possibly target protein identity (Kaloshian & Walling 2016b).

Until recently, there was no direct evidence that insect effectors are transported into specific plant tissues and cells. Mugford *et al.* (2016) demonstrated for the first time that insect (aphid) effectors are delivered into the cytosol of plant cells during probing in the pathway phase, and other effectors are embedded within the sheaths that surround stylets in the apoplastic space of mesophyll tissue. Therefore, we might surmise that Si deposited within the apoplastic space interferes with such feeding styles. This could explain, at least in part, why, in Si-treated plants, we often observe piercing and sucking insects showing reduced probing time, although not necessarily increased mortality (Goussain *et al.*, 2005; Costa *et al.*, 2011). Thus, similar to the case proposed for pathogens, effectors released by insects could be trapped within the extracellular Si matrix, preventing them from impeding the plant defence response, or from recognising the plant as a suitable host (Hogenhout & Bos, 2011).

V. Silicon and abiotic stress: a proliferation of proposed mechanisms

Remarkably, Si has been reported to alleviate a wide range of abiotic stresses, including radiation (Shen *et al.*, 2010), lodging (Savant *et al.*, 1997), wounding (Kim *et al.*, 2014), temperature (Muneer *et al.*, 2017), hypoxia (Fleck *et al.*, 2011), salinity (Flam-Shepherd *et al.*, 2018), drought (Liu *et al.*, 2014), nutrient deficiency, such as that of iron (Fe; Pavlovic *et al.*, 2016), P (Kostic *et al.*, 2017), and K (Chen *et al.*, 2016), and heavy-metal toxicity (e.g. cadmium (Cd), Shao *et al.*, 2017; manganese (Mn), Che *et al.*, 2016; arsenic (As), Sanglard *et al.*, 2014; aluminum (Al), Wang *et al.*, 2004; and copper (Cu), Mateos-Naranjo *et al.*, 2015). Although some of these stresses are related, this is a diverse and largely disparate set of scenarios, and so it stands to reason that Si is providing some fundamental protection to plants that confers a wide range of benefits. Perplexingly, a survey of the relevant literature appears to suggest otherwise, with Si seemingly involved in a plethora of processes and functions, including gene expression (Manivannan & Ahn, 2017), redox homeostasis and oxidative stress (Liang *et al.*, 2003; Zhu *et al.*, 2004; Farooq *et al.*, 2016), nitrogen assimilation (Pereira *et al.*, 2013), carbohydrate metabolism (Zhu *et al.*, 2016), cell signaling (Detmann *et al.*, 2012, 2013), transmembrane ion and water fluxes (Liang *et al.*, 2006; Liu *et al.*, 2014), hormone regulation (X. L. Liang *et al.*, 2015; Markovich *et al.*, 2017), root exudation (Kidd *et al.*, 2001; Wu *et al.*, 2016), heavy-metal chelation (Wang *et al.*, 2004; Ma *et al.*, 2015), root architecture (Gong *et al.*, 2006; Fleck *et al.*, 2011), transpiration (Gao *et al.*, 2006), and photosynthesis (Shen *et al.*, 2010; Detmann *et al.*, 2012) (for reviews, see Epstein, 1999; Ma, 2004; Liang *et al.*, 2007; Meharg & Meharg, 2015; Cooke & Leishman, 2016; Coskun *et al.*, 2016; Debona *et al.*, 2017; Frew *et al.*, 2018).

Oxidative stress is a hallmark feature of stress (Mittler, 2002; Apel & Hirt, 2004; Gill & Tuteja, 2010) and its reduction by Si, by upregulating antioxidant activity, is a proposed major mode of action (Liang, 1999; Liang *et al.*, 2003, 2006; Zhu *et al.*, 2004; Gong *et al.*, 2005; Gunes *et al.*, 2007; Farooq *et al.*, 2016; Hasanuzzaman *et al.*, 2017; Kim *et al.*, 2017; cf Mateos-Naranjo *et al.*, 2015). Consequently, several studies have linked Si with elevated shoot and root activities of antioxidants, both enzymatic (e.g. superoxide dismutase, peroxidase, catalase, ascorbate peroxidase, and glutathione reductase) and non-enzymatic (e.g. ascorbate, glutathione, phenolic compounds, etc.), as well as changes in the concentrations of common markers of oxidative stress, including malondialdehyde, hydrogen peroxide (H_2O_2), and proline, under various abiotic stresses (for review see Liang *et al.*, 2007; Cooke & Leishman, 2016; Kim *et al.*, 2017). Once again, however, one must be cognizant of the points of reference and the distinctions between direct and indirect effects. Indeed, compared to stress conditions without Si supplementation, Si does appear to alleviate oxidative stress, which, however, does not mean that Si is directly involved in antioxidant activity, and, in fact, no such evidence presently exists. Moreover, as with other biochemical processes (see Section III), Si has no clear or consistent effect on antioxidant activity in the absence of stress (Table 1). Thus, a more parsimonious explanation is that Si is preventing or mitigating the strains imposed by stress, which is, then, reflected in a reduced induction of oxidative stress (Fig. 4a). This is perhaps most clearly supported by the fact that Si supply consistently reduces the root-to-shoot translocation of toxicants (e.g. Na, As, Mn, and Cd) and, thus, their cellular accumulation in leaf tissues (Yeo *et al.*, 1999; Gong *et al.*, 2006; Sanglard *et al.*, 2014; Che *et al.*, 2016; Shao *et al.*, 2017; Flam-Shepherd *et al.*, 2018; cf Rogalla & Römheld, 2002; Blamey *et al.*, 2018). A reduction in toxicant accumulation will obviously reduce the strains imposed on shoot tissues and thus be reflected in reduced oxidative stress.

Reactive oxygen species (ROS) are central to cell signaling and influence a wide range of critical and cascading processes, including the expression of genes, growth, development, programmed cell death, and a suite of stress responses (Mittler, 2002; Apel & Hirt, 2004; Gill & Tuteja, 2010). Thus, it is no surprise that reductions in ROS with Si provision, under stress conditions, result in numerous downstream changes (Y. Liang *et al.*, 2003, 2005, 2015; Zhu *et al.*, 2004; Yin *et al.*, 2016; Markovich *et al.*, 2017); however, this should not be confused with an ‘active role’ of Si. For example, Si supplementation has been claimed to influence many physiological parameters based on correlations with elevated polyamine levels (e.g. spermidine, spermine, and putrescine) and reduced ethylene signaling in salt-stressed sorghum (Yin *et al.*, 2016), but such observations are far from conclusive in terms of mechanistic evidence. Likewise, claims that Si alleviates K^+-deficiency-induced leaf chlorosis by decreasing the accumulation of putrescine is unsubstantiated (Chen *et al.*, 2016). A similar conclusion can be drawn from a recent analysis of silicon's role in promoting cytokinin biosynthesis and its relationship with delaying senescence in Arabidopsis and sorghum (Markovich *et al.*, 2017). Another common claim is that Si can influence the transport of water and ions across membranes. For example, in the context of hyperosmotic stress, increases in hydraulic conductivity with Si provision have been ascribed to increased expression of genes encoding AQPs (Liu *et al.*, 2014). Similarly, with salinity (NaCl) stress, some studies have suggested that Si can promote the vacuolar sequestration of Na^+ and, thus, protect vital cytoplasmic functions (Liang *et al.*, 2007, and references therein). This is largely based on observations of increased H^+-ATPase activities with Si provision (Liang, 1999; Liang *et al.*, 2005, 2006) and speculations on downstream effects on H^+-dependent Na^+ fluxes (e.g. tonoplast (NHX1) or plasma-membrane (SOS1) antiporters). Again, these results are correlative and only observed under stress, as opposed to control conditions, suggesting that, rather than stimulating AQP function or H^+-ATPase activity, Si is simply mitigating their decrease (Fig. 4a). As far as we are aware, the only attempts to directly measure the effect of Si on root Na^+ fluxes yielded no observable effects in salt-stressed rice seedlings (Malagoli *et al.*, 2008; Flam-Shepherd *et al.*, 2018). Similarly, electrophysiological measurements conducted in epidermal and cortical root cells demonstrated no effects of Si provision on resting membrane potentials or NaCl-induced depolarizations, suggesting that Si has no effect on transmembrane currents (Flam-Shepherd *et al.*, 2018). With respect to other toxicants, claims that Si inhibits transmembrane Cd influx and stimulates vacuolar sequestration similarly lack mechanistic evidence (Ma *et al.*, 2016). In the context of nutrient deficiency, the claim that Si increases P influx in P-deprived wheat, based on gene-expression analyses (i.e. increases in expression for genes encoding P transporters) and tissue content data, does not offer evidence of a direct involvement of Si in the process (Kostic *et al.*, 2017). Although such proposals cannot be entirely ruled out, caution must always be applied when using changes in gene expression to act as a proxy for changes in protein abundance or activity without proper verification (Tian *et al.*, 2004; Schwanhausser *et al.*, 2011; Ponnala *et al.*, 2014).

What could explain such widespread effects, then, if they only reflect downstream (indirect) responses? In other words, what are the ultimate causes of Si-provided alleviation of abiotic stress? In the case of shoot tissues, Si deposition in cuticles has been shown to prevent water loss via evapotranspiration, protecting plants faced with water deficits (Ma *et al.*, 2001; Ma, 2004). In roots, Si accumulates around cells expressing Si transporters, such as the exodermis and endodermis in rice (Lux *et al.*, 2003; Gong *et al.*, 2006; Ma & Yamaji, 2015). This is critical because Si deposition surrounding these cell layers blocks the 'apoplastic bypass route', whereby ions such as Na^+, Cl^-, and Cd^{2+} enter the transpiration stream via breaks and underdevelopments in the Casparian band (CB), and subsequently accumulate in shoots, potentially to toxic levels (Yeo *et al.*, 1999; Ranathunge *et al.*, 2005; Shi *et al.*, 2005, 2013; Gong *et al.*, 2006; Faiyue *et al.*, 2010; Flam-Shepherd *et al.*, 2018). Interestingly, Si appears to not only 'clog up' apoplastic bypass routes, but it also appears to promote CB formation itself by contributing to the stimulation of suberin and lignin biosynthesis, thus further protecting plants against apoplastic bypass of toxicants (Fleck *et al.*, 2011, 2015). The mechanism by which these changes occur are not yet clear, although it is hypothesized that Si interacts and crosslinks with phenols within cell walls or induces precipitation of phenols leading to enhanced CB development. Lastly, the co-precipitation of Si and heavy-metal toxicants such as Al in the extracellular matrix is another critical consideration (Kidd *et al*., 2001; Wang *et al*., 2004; Ma *et al*., 2015; Wu *et al*., 2016).

VI. The apoplastic obstruction hypothesis: a working model

While the last 25 years have seen an unprecedented amount of research into the roles of Si in plant biology, it appears that a number of hypotheses nearly commensurate with the number of studies have been proposed, which has exacerbated the confusion. For instance, in a recent review describing the putative effects of Si, Frew *et al.* (2018) identified an inordinate amount of reported effects under various environmental conditions, including cell signaling, amino-acid metabolism, photosynthesis, cell growth and division, and transcriptomic processes, which, taken as a whole, are incongruent with what we know about the properties of Si. Thus, in trying to propose a hypothesis to define the role of Si, we have taken a holistic and parsimonious approach, encompassing the various scenarios described in the literature in line with chemical and biological realities.

The first premise we considered was the evidence against a nutritional role for Si. As argued in this review, this position is supported by the vast majority of scientific papers, as well as the IPNI and most regulation agencies throughout the world. This perspective is not trivial because whether or not Si is accepted as a plant nutrient has direct repercussions on how its role is viewed in situations of stress. It is indeed unlikely that, if an element has no effect on a plant's metabolism in unstressed conditions, it would suddenly acquire unsuspected properties when a stress is imposed.

The second premise relates to the chemistry and biochemistry of $Si(OH)_4$, the soluble form of Si absorbed by plants. As outlined in Section I, $Si(OH)_4$ is uncharged and unreactive in cells (Exley, 2015); therefore, it stands to reason that there are no biochemical roles for $Si(OH)_4$ in terms of interactions with enzymes or other intracellular constituents; claims to that effect have been based on indirect effects and correlative evidence. As discussed here, the concept that $Si(OH)_4$ *in planta*, as a minor unpolymerized fraction, could play a cellular role was first suggested by Fawe *et al.* (2001), invoking the role of a secondary messenger inducing defence responses. As a result, this notion was extended to other forms of stress, but remained speculative and unsubstantiated until Vivancos *et al.* (2015) provided definitive evidence that $Si(OH)_4$ did not have a role as a signaling molecule or secondary messenger. Thus, the position that Si would have diverse and complex biochemical roles is untenable, particularly if one juxtaposes the numerous mechanistic proposals with the lack of direct evidence. It is our opinion that the expansion of mechanistic claims can largely be explained by the fallacy of conflating correlation with causation.

On the basis of these assumptions and the many benefits observed in Si-supplied plants, we conclude that the different forms of stress alleviation mediated by Si, whether biotic or abiotic, mostly stem from a common mechanism, referred to here as the apoplastic obstruction hypothesis. Under this scheme, the amorphous Si portion that deposits in the apoplast both interferes with and promotes a number of biological events leading to its beneficial role (Fig. 5). In the case of biotic stress, it interferes with the recognition process establishing the specificity between a plant and a fungal pathogen or insect, by altering the flow of the arsenal of molecules (e.g. effectors) and the establishment of structures such as the haustorium at the membrane interface a parasite uses to attack a plant (Fig. 5). On many levels, this explains the specificity of pathogens controlled by Si, and why those with a biotrophic phase (i.e. producing a haustorium) are particularly associated with the prophylactic properties of Si. In the case of abiotic stress, Si deposits around and fortifies apoplastic barriers surrounding the vasculature, and thus precludes the transport and accumulation of toxicants into the shoot, thereby preventing or mitigating downstream stress events (Fig. 5). Moreover, Si can co-precipitate with toxicants in the extracellular matrix, thus protecting tissues against stress (Kidd *et al.*, 2001; Rogalla & Römheld, 2002; Wang *et al.*, 2004; He *et al.*, 2013, 2015; Pavlovic *et al.*, 2013; Ma *et al.*, 2016; Wu *et al.*, 2016). Lastly, Si deposition in cuticles will prevent water loss, which is particularly important under osmotic stress.

VII. Perspectives and conclusions

Explaining the roles of Si in plant biology has remained a quandary since the mechanisms that have been proposed to explain the large number of reported beneficial effects are seemingly at odds with its rather limited biochemical properties. There is also a disparity between its current practical exploitation in agriculture as a fertilizer and all the potential advantages it could confer, as large-scale applications are the exception rather than the norm. Accordingly, if we are to effectively benefit from its use, it is important to correctly understand the mechanistic underpinnings of its biological role in plants.

As detailed in this review, there are many intricacies inherent to the properties of Si, and, as such, a generic acceptance of the multitude of mechanistic proposals applied to plants can only lead to confusion, unfounded expectations, and negative results. First and foremost, it is important to recognize that plants differ widely in their ability to take up Si from the external environment, and concomitantly, differ widely in the benefits they derive from Si. Classifying plants on the basis of Si accumulation in the field can often lead to false conclusions as soil properties, plant-available Si, and plant development can greatly influence phenotypes. The precise description of functional elements of Si transporters has made it possible to rely on molecular tools to classify plants as accumulators and non-accumulators, and as genomic data become routinely available, they should be exploited to precisely categorize plants on the basis of the presence of functional Si transporters.

The preponderance of the scientific evidence is in favour of the argument that the nutritional role of Si is rather a proxy of stress alleviation, and suggests, at the very least, restraint when linking Si and nutrition. On the other hand, the benefits of Si under conditions of stress appear to be unanimously accepted. Biotic stresses have been particularly well documented in the case of fungal pathogens that possess a biotrophic phase, as well as with some insects. The fact that there is a level of specificity with respect to the parasites controlled by Si also supports arguments for a simple mode of action. In terms of abiotic stresses, the list of Si-induced protections grows continuously, which has prompted a proliferation of possible biochemical roles for Si. However, most of the roles appear to be associated with a prevention of the deregulation inherent to the stress itself, i.e. are indirect, rather than direct, effects. Given that crops in agricultural practice will always grow under some form of stress, the debate on whether the effects of Si are limited to stressed conditions may, of course, ultimately be moot, and it may well be that future recommendations to agronomists will include Si applications to fields that are deficient in the element (Y. Liang *et al.*, 2015), in particular with a view to the rapid pace of global climate change and the increased incidence of inclement and extreme weather events (Lobell *et al.*, 2011; Cai *et al.*, 2014; Myers *et al.*, 2014).

Taken together, we propose a unifying model, termed the apoplastic obstruction hypothesis, by which Si can exert its multitude of beneficial effects (Fig. 5). Through this model, our aim is to stimulate critical thinking and positive advances toward a better understanding of Si properties. Recent advances have contributed to elevate Si to the status of beneficial substance, and our hope is that continued efforts will guide research in the direction of mechanistic elucidation and biotechnological advancements for an optimal exploitation of Si in agricultural practice.

Acknowledgements

This work was supported by a Postdoctoral Fellowship to D.C. and grants to R.R.B from the Natural Sciences and Engineering Research Council of Canada (NSERC). It was further supported by the University of Melbourne (to H.J.K.) and grants from the Fonds de Recherche du Québec-Nature et Technologies (FRQNT) to R.R.B., the Grant-in-Aid for Specially Promoted Research (JSPS KAKENHI Grant Number 16H06296 to J.F.M.), and the Canada Research Chairs (CRC) Program to R.R.B. The authors also thank Malcom Keeping for his critical review of the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Table S1 Detailed list of studies reported in Table 2

Fig. 1 Number of silicon (Si)-related publications in the plant sciences from 1934 to 2017 (based on *Web of Science* search with the words 'silicon' or 'silicate' or 'silicic' in the title, and refined to the 'Plant Sciences' category).

Fig. 2 Leaf silicon (Si) content is dependent on rootstock genotype. (a) Schematic representation of grafting method. (b) The effect of rootstock genotype on Si accumulation in leaves of four separate soybean scions (taken from Bélanger *et al*., 2016). Error bars denote ± SEM.

Fig. 3 Molecular characterization and phylogeny of the silicon (Si) channel, Lsi1. (a) Simplified 2D structure of TaLsi1 from wheat showing all known features that influence solute specificity (see key). (b) 3D model of TaLsi1. (c) Phylogenetic tree of all Nodulin 26-like intrinsic proteins (NIPs) identified in *Arabidopsis thaliana* (At), *Brassica rapa* (Br), *Brachypodium distachyon* (Bd), poplar (*Populus trichocarpa*, Pt), and rice (*Oryza sativa*, Os), highlighting the presence of NIP-IIIs (of which Lsi1 belongs to) only in Si-accumulating species. (d) Taxonomical distribution of high- and low-Si-accumulating species, and their leaf Si content (in % DW).

Fig. 4 Silicon (Si) effects (or lack thereof) under experimentally controlled stress-free conditions. (a) Generalized representation of Si effects on biochemical/physiological variables (e.g. growth, photosynthesis, enzyme activity, etc.) under control (stress-free) and stress conditions (for details, see Sections III and V, Table 1). Note, under stress, Si effects can range from no benefit to complete recovery (see light blue bar). (b) Transcriptomic analyses of Si effects under control (C; stress-free) conditions in soybean (as measured by RNA-seq; Rasoolizadeh *et al*., 2018) and Arabidopsis and wheat (as measured by microarray; Fauteux *et al*., 2006; Chain *et al*., 2009). Note, for microarray data, a cut-off of $\log_2$ fold-change was considered; thus, based on this analysis, only two (out of *c*. 28500 transcripts) and 47 (out of *c*. 55000 transcripts) differentially expressed genes (DEGs) were found in Arabidopsis and wheat, respectively (see Section III for details).

Fig. 5 The apoplastic obstruction hypothesis. (a) In roots, toxicants (X) can take both symplastic and apoplastic routes towards the stele (see black arrows). The apoplastic path is blocked by the Casparian band (CB), although breaks may occur which allow for bypass routes, particularly under low-silicon (-Si) conditions (Yeo *et al*., 1999; Gong *et al*., 2006). By contrast, high-silicon (+Si) plants have improved CB development (Fleck *et al*., 2011), as well as apoplastic Si deposition (as silica, SiO_2; Gong *et al*., 2006), effectively blocking bypass routes, and thus, root-to-shoot translocation of toxicants. Red arrows denote symplastic and xylem transport of Si (as silicic acid, $Si(OH)_4$; Ma & Yamaji, 2015). (b) With abiotic stress, toxicant levels in shoots accumulate to a greater extent in -Si plants relative to +Si plants (as a function of SiO_2 deposition in roots; see (a)), resulting in elevated reactive oxygen species (ROS), and thus increased oxidative stress (e.g. decreased membrane stability (MS), decreased enzyme activity (EA), etc.), changes in gene expression, as well as decreased growth and function (e.g. photosynthesis, Ps). In +Si plants, ROS are limited and detoxified, resulting in less stress and increased growth, relative to -Si plants. Apoplastic Si deposition (SiO_2) in shoots can also aid in the prevention of ultraviolet radiation (UV) damage and water (H_2O) loss via evapotranspiration. (c) Under pathogenic-fungal attack, -Si plants are susceptible to fungal invasion and development of haustorial bodies (HB), whereas +Si plants would be protected as a result of apoplastic Si deposition (SiO_2) interfering with effector (eff) release, translocation to the cytoplasm (Cyt), and/or host recognition and effector-receptor (e.g. receptor-like kinase (RK)) interactions (Rasoolizadeh *et al*., 2018). Susceptibility in -Si conditions will correspond to effectors effectively blocking plant defence responses (DR). Micrographs under -Si and +Si panels demonstrate healthy and collapsed HB, respectively (taken from Ghanmi *et al*., 2004). Cu, cuticle; Apo, apoplast; PM, plasma membrane; EHM, extrahaustorial matrix. (d) A similar scenario to (c) may play out under insect (e.g. piercing-sucking type) attack, resulting in decreased release and translocation of effectors in +Si relative to -Si plants.

Table 1 Literature survey of the biochemical/physiological effects of silicon (Si) supplementation

Stress	**Reference**	**Species**	**Growth condition (Treatment)**	**Variable**	**Si effect (without stress)?**	**Si effect (with stress)?**
Fungal disease	Cai *et al*. (2008)	Rice (*Oryza sativa*)	Vermiculite (+/- rice blast; *Magnaporthe grisea*)	Lignin content	No	Yes
				POD activity	No	Yes
				PPO activity	No	Yes
				PAL activity	No	Yes
	Gao *et al*. (2011)	Rice (*O. sativa*)	Vermiculite (+/- rice blast)	Mineral nutrient content	No	Yes
				Chlorophyll content	No	No
				F_v/F_m	No	Yes
				F_v/F_0	No	Yes
	Resende *et al*. (2012)	Sorghum (*Sorghum bicolor*)	Hydroponics (+/- anthracnose; *Colletotrichum sublineolum*)	A_{net}	No	Yes
				g_s	No	Yes
				$C_i : C_a$	No	Yes
				E	No	Yes
				SOD activity	No	Yes

				CAT activity	No	Yes
				APX activity	No	Yes
				GR activity	No	Yes
				Leaf electrolyte leakage	No	Yes
				H_2O_2 content	No	Yes
				MDA content	No	Yes
Salinity	Zhu *et al*. (2004)	Cucumber (*Cucumis sativus*)	Hydroponics (+/- 50 mM NaCl)	Total DW	Yes	Yes
				Leaf soluble protein content	No	Yes
				Root electrolyte leakage	No	Yes
				Lipid peroxidation	No	Yes
				H_2O_2 content	Yes	Yes
				SOD activity	No	Yes
				GPX activity	No	Yes
				APX activity	No	Yes
				DHAR activity	No	Yes
				GR activity	No	Yes
				CAT activity	No	Yes

	Yin *et al*. (2016)	Sorghum (*S. bicolor*)	Hydroponics (+/- 100 mM NaCl)	Total DW	No	Yes
				Chlorophyll content	No	Yes
				Shoot Na^+ content	No	Yes
				Root Na^+ content	No	No
				Root K^+ content	No	No
				Total polyamine content	Yes	Yes
				Total ACC content	No	Yes
	Flam-Shepherd *et al*. (2018)	Rice (*O. sativa*)	Hydroponics (+/- 35 or 50 mM NaCl)	Shoot DW	Yes	Yes
				Shoot Na^+ content	No	Yes
				E	nd	Yes
				Apoplastic bypass flow	nd	Yes
				Root membrane electrical potential	No	No
				Na^+ influx	No	No
				Na^+ efflux	No	No
Osmotic	Hattori *et al*.	Sorghum (*S.*	Hydroponics (+/-	A_{net}	No	Yes

	(2008)	*bicolor*)	10% PEG-6000)			
				g_s	No	Yes
				E	No	Yes
				Root hydraulic resistance	No	Yes
	Liu *et al*. (2014)	Sorghum (*S. bicolor*)	Hydroponics (+/- 10% PEG-6000)	Total DW	No	Yes
				A_{net}	No	Yes
				g_s	No	Yes
				E	No	Yes
				Leaf RWC	No	Yes
				Leaf water potential	No	Yes
				K_{plant}	No	Yes
				Root xylem potential	No	No
				L_p	No	Yes
				Root surface area	No	No
	Shi *et al*. (2016)	Tomato (*Solanum lycopersicum*)	Hydroponics (+/- 10% PEG-6000)	Total DW	No	No
				Root : shoot ratio	No	No
				A_{net}	No	Yes

				E	Yes	Yes
				Leaf water content	No	Yes
				L_p	No	Yes
				Root electrolyte leakage	No	Yes
				MDA content	No	Yes
				H_2O_2 content	No	Yes
				SOD activity	No	Yes
				CAT activity	No	Yes
				Ascorbic acid content	Yes	Yes
				GSH content	No	Yes
Cd toxicity	Farooq *et al*. (2016)	Rice (*O. sativa*)	Hydroponics (+/- 10 µM Cd)	Total DW	No	Yes
				ΦPSII	No	Yes
				Leaf H_2O_2 content	Yes	Yes
				Root H_2O_2 content	No	Yes
				Leaf ascorbate content	Yes	Yes
				Root ascorbate	No	Yes

				content		
				Leaf GSH content	Yes	Yes
				Root GSH content	No	Yes
				Leaf NPT content	Yes	Yes
				Root NPT content	No	Yes
	Wu *et al*. (2016)	Wheat (*Triticum aestivum*)	Hydroponics (0–25 µM Cd)	Oxalate root exudation	No	Yes
As toxicity	Sanglard *et al*. (2014)	Rice (*O. sativa*)	Hydroponics (+/- 25 µM As)	A_{net}	No	Yes
				g_s	No	Yes
				g_m	No	Yes
				V_{cmax}	No	No
				J_{max}	No	No
				$J_o : J_c$	No	Yes
				F_v/F_m	No	No
				q_p	No	No
Mn toxicity	Rogalla & Römheld (2002)	Cucumber (*C. sativus*)	Hydroponics (+/- 50 µM Mn)	Shoot FW	No	Yes
				Root FW	No	Yes
				Leaf Mn content	No	No
	Maksimović *et al*. (2012)	Cucumber (*C. sativus*)	Hydroponics (+/- 100 µM Mn)	Shoot DW	Yes	Yes

				Root DW	Yes	Yes
				Leaf Mn content	No	Yes
				H_2O_2 content	No	Yes
				GPX activity	Yes	Yes
Al toxicity	Wang *et al*. (2004)	Maize (*Zea mays*)	Hydroponics (+/- 25 or 100 µM Al)	Root elongation	No	Yes
				Root length	No	Yes
				Root citrate exudation	No	No
				Root malate exudation	No	No
				Root total phenol exudation	No	No
Cu toxicity	Mateos-Naranjo *et al*. (2015)	*Spartina densiflora*	Hydroponics (+/- 15 mM Cu)	Shoot FW	No	No
				Root FW	No	Yes
				RGR	No	Yes
				No. of tillers	No	Yes
				A_{net}	No	Yes
				g_s	No	Yes
				C_i	No	Yes
				iWUE	No	Yes

				ΦPSII	No	Yes
				Chlorophyll content	No	Yes
				Rubisco content	No	Yes
				Rubisco carbamylation	No	No
				TSP content	No	Yes
				Total respiration (O_2 isotope fractionation)	No	No
				Total respiration (O_2 electrode)	No	Yes
K^+ deficiency	Chen *et al*. (2016)	Sorghum (*S. bicolor*)	Hydroponics (0.05 (low) or 3 mM K^+ (high))	Total DW	No	Yes
				A_{net}	No	Yes
				F_v/F_m	No	Yes
				Soluble protein content	No	Yes
				Chlorophyll content	No	Yes
				Chl*a*/*b*	No	Yes
				Leaf K^+ content	No	No

				Leaf polyamine content	No	Yes
				Leaf arginine content	No	Yes
				DAO activity	No	Yes
				PAO activity	No	Yes
				H_2O_2 content	No	Yes
				SOD activity	No	Yes
				CAT activity	No	Yes
				APX activity	No	Yes

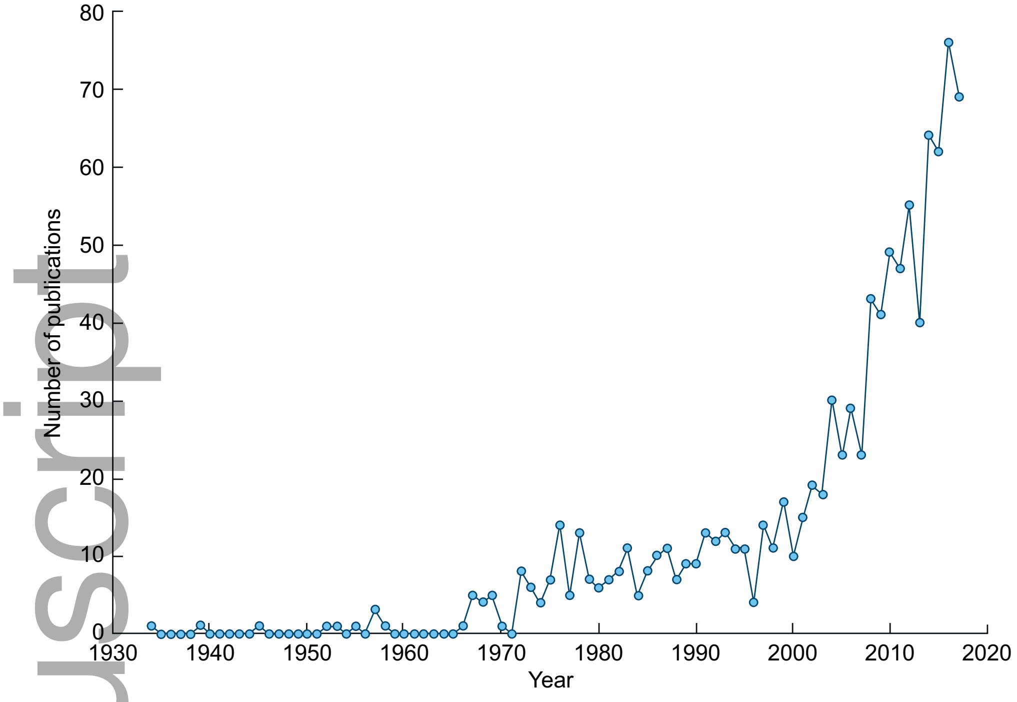
ACC, 1-aminocyclopropane-1-carboxylic acid; A_{net}, net carbon assimilation rate; APX, ascorbate peroxidase; CAT, catalase; $C_i : C_a$, internal to ambient CO_2 concentration ratio; DAO, diamine oxidase; DHAR, Dehydroascorbate reductase; E, transpiration rate; F_v/F_0, ratio of variable to minimum fluorescence; F_v/F_m, ratio of variable to maximum fluorescence; g_m, mesophyll conductance; GPX, guaiacol peroxidase; GR, glutathione reductase; g_s, stomatal conductance; GSH, reduced glutathione; iWUE, instantaneous water-use efficiency; J_{max}, maximum rate of carboxylation limited by electron transport; $J_o : J_c$, ratio of electron transport rate devoted to oxygenation/carboxylation; K_{plant}, whole plant hydraulic conductance; L_p, root hydraulic conductance; MDA, malondialdehyde; nd, not determined; NPT, non-protein thiols; PAL, phenylalanine ammonia-lyase; PAO, polyamine oxidase; POD, peroxidase; PPO, polyphenol oxidase; q_p, photochemical quenching coefficient; RGR, relative growth rate; RWC, relative water content; V_{cmax}, maximum rate of carboxylation; ΦPSII, steady-state quantum yield of photosystem II.

Table 2 Number of studies suggesting beneficial effects of silicon (Si) in different plant species against biotrophic, hemibiotrophic, and necrotrophic fungi

Pathogen	**Number of studies**[a]
Biotroph/Hemibiotroph	100
Necrotroph	8
*Bipolaris oryzae**	11

[a] For a detailed breakdown of the studies, refer to Supporting Information Table S1.

*Host-specific necrotroph.



80
70
60
50
40
30
20
10
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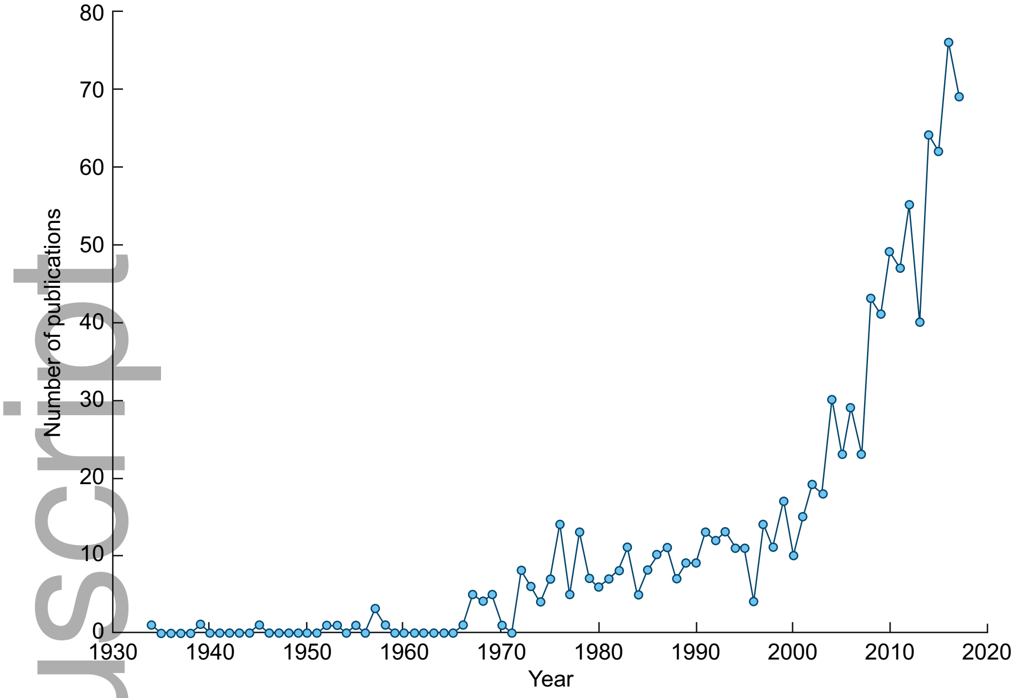
Number of publications
1930
1940
1950
1960
1970
1980
1990
2000
2010
2020
Year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Number of publications
1930
1940
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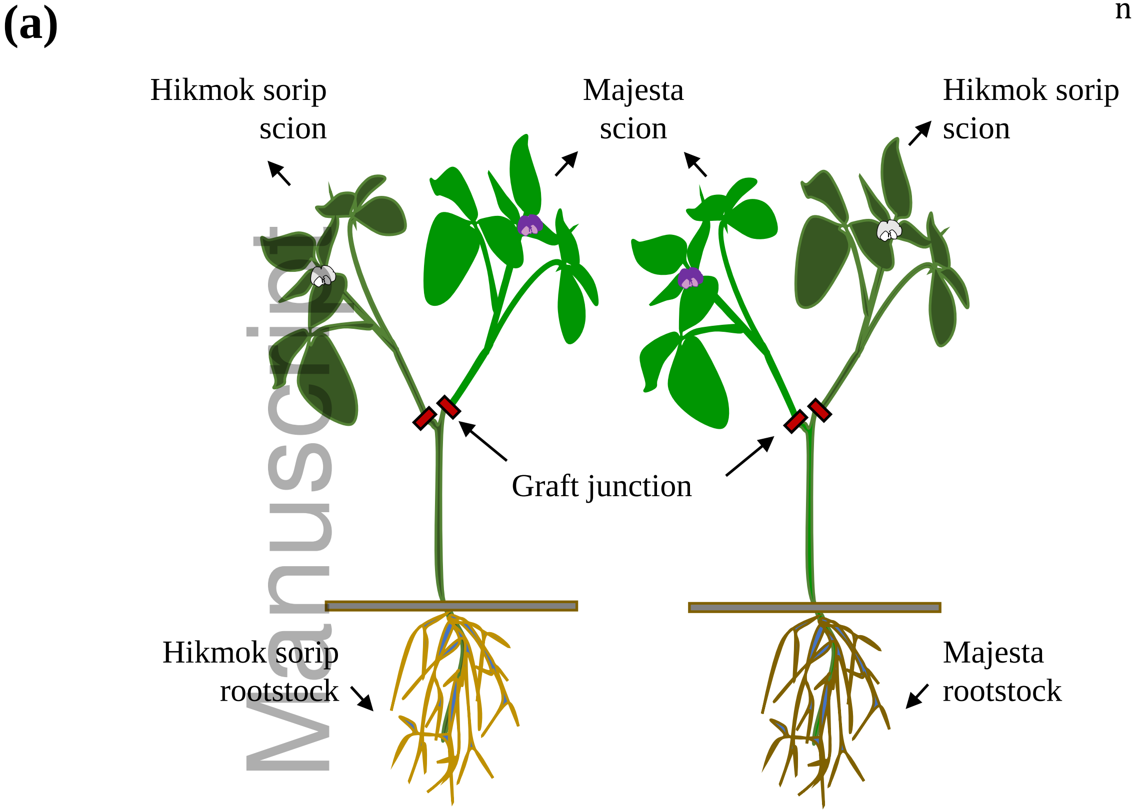
2020
Year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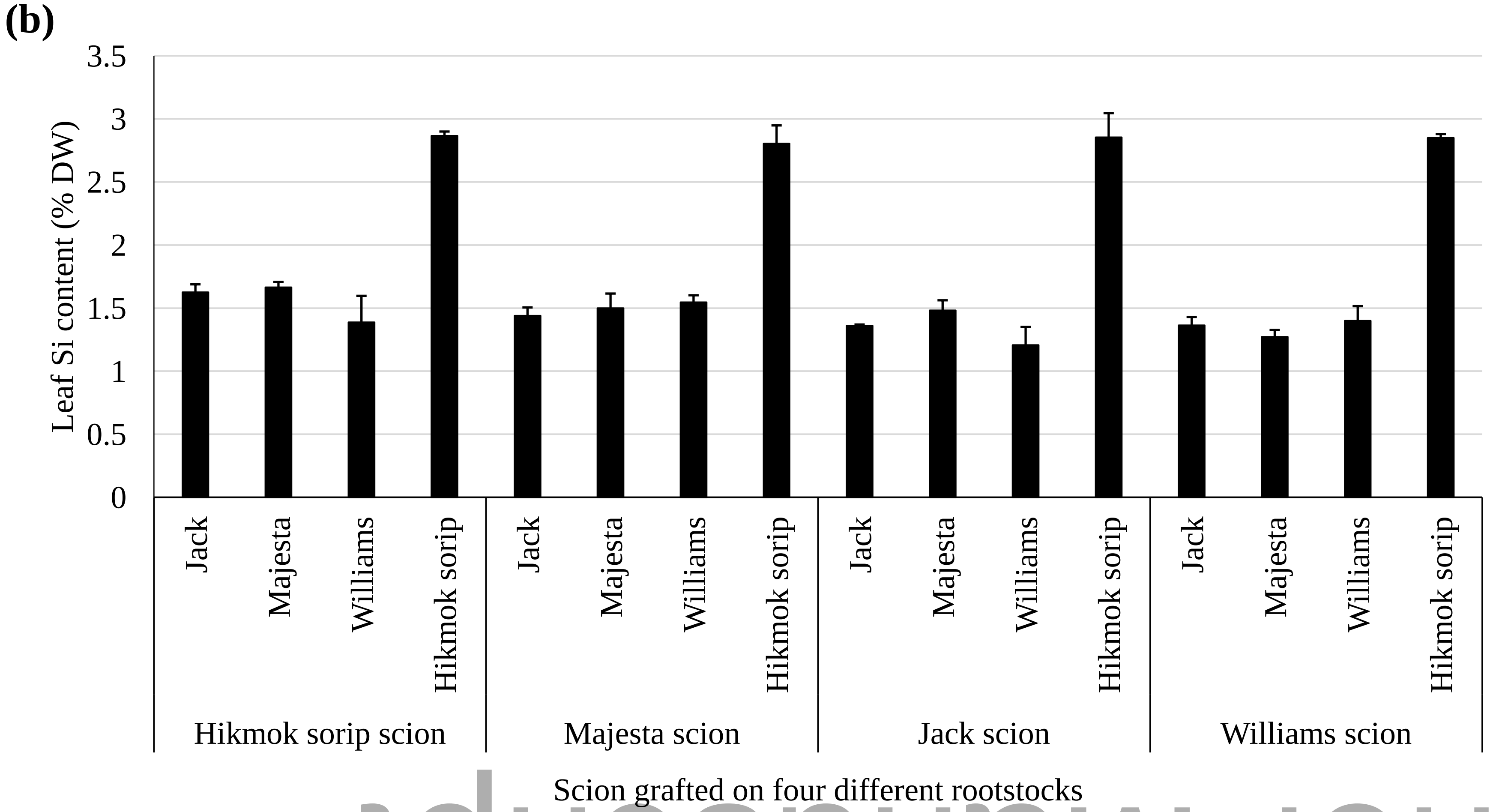
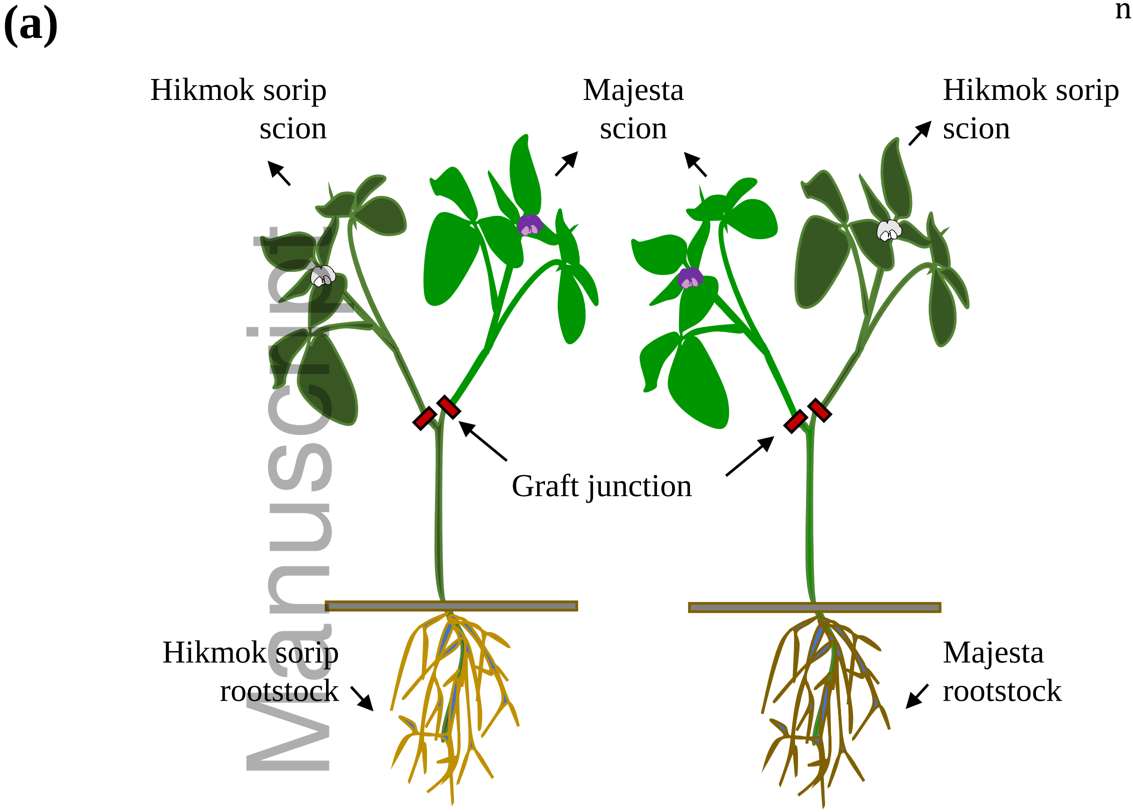
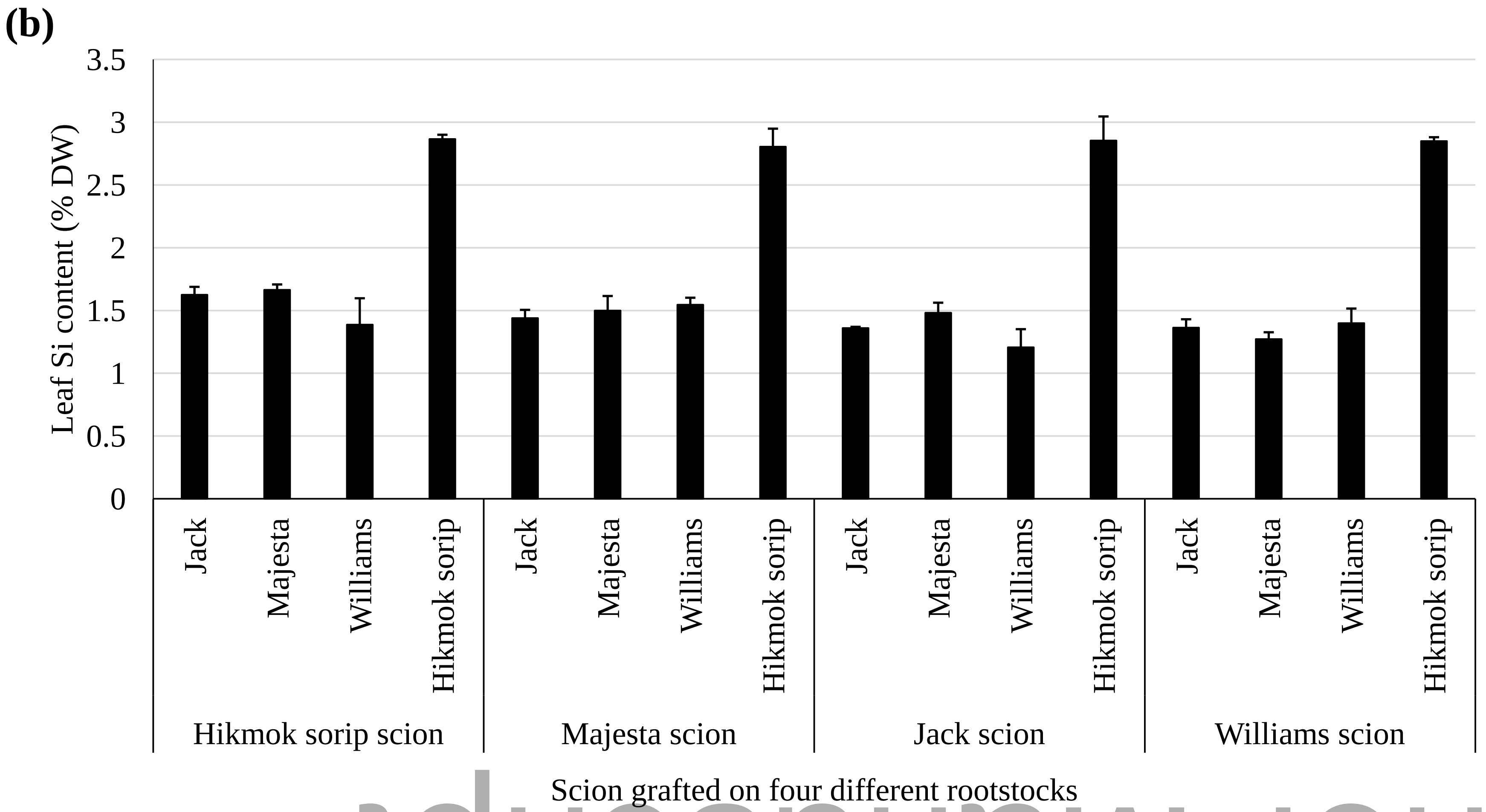
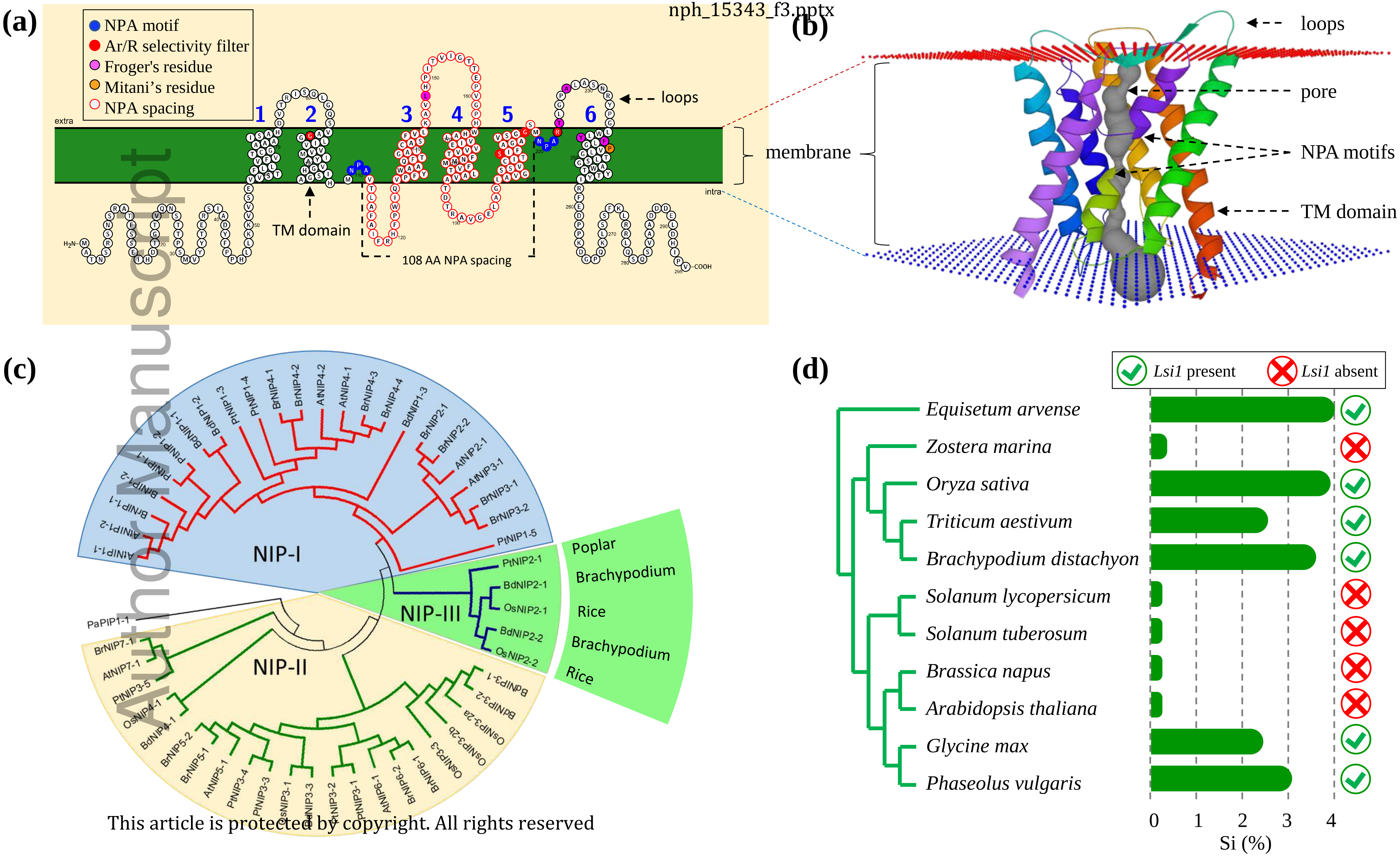
Majesta scion
Hikmok sorip scion
Graft junction
Hikmok sorip rootstock
Majesta rootstock


(b)
Leaf Si content (% DW)
0
0.5
1
1.5
2
2.5
3
3.5
Jack
Majesta
Williams
Hikmok sorip
Hikmok sorip scion
Jack
Majesta
Williams
Hikmok sorip
Majesta scion
Jack
Majesta
Williams
Hikmok sorip
Jack scion
Jack
Majesta
Williams
Hikmok sorip
Williams scion
Scion grafted on four different rootstocks


(a)
Hikmok sorip
scion
Majesta
scion
Hikmok sorip
scion
Graft junction
Hikmok sorip
rootstock
Majesta
rootstock


(b)
Leaf Si content (% DW)
3.5
3
2.5
2
1.5
1
0.5
0
Jack
Majesta
Williams
Hikmok sorip
Hikmok sorip scion
Majesta scion
Jack scion
Williams scion
Scion grafted on four different rootstocks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NPA motif
Ar/R selectivity filter
Froger's residue
Mitani's residue
NPA spacing
extra
intra
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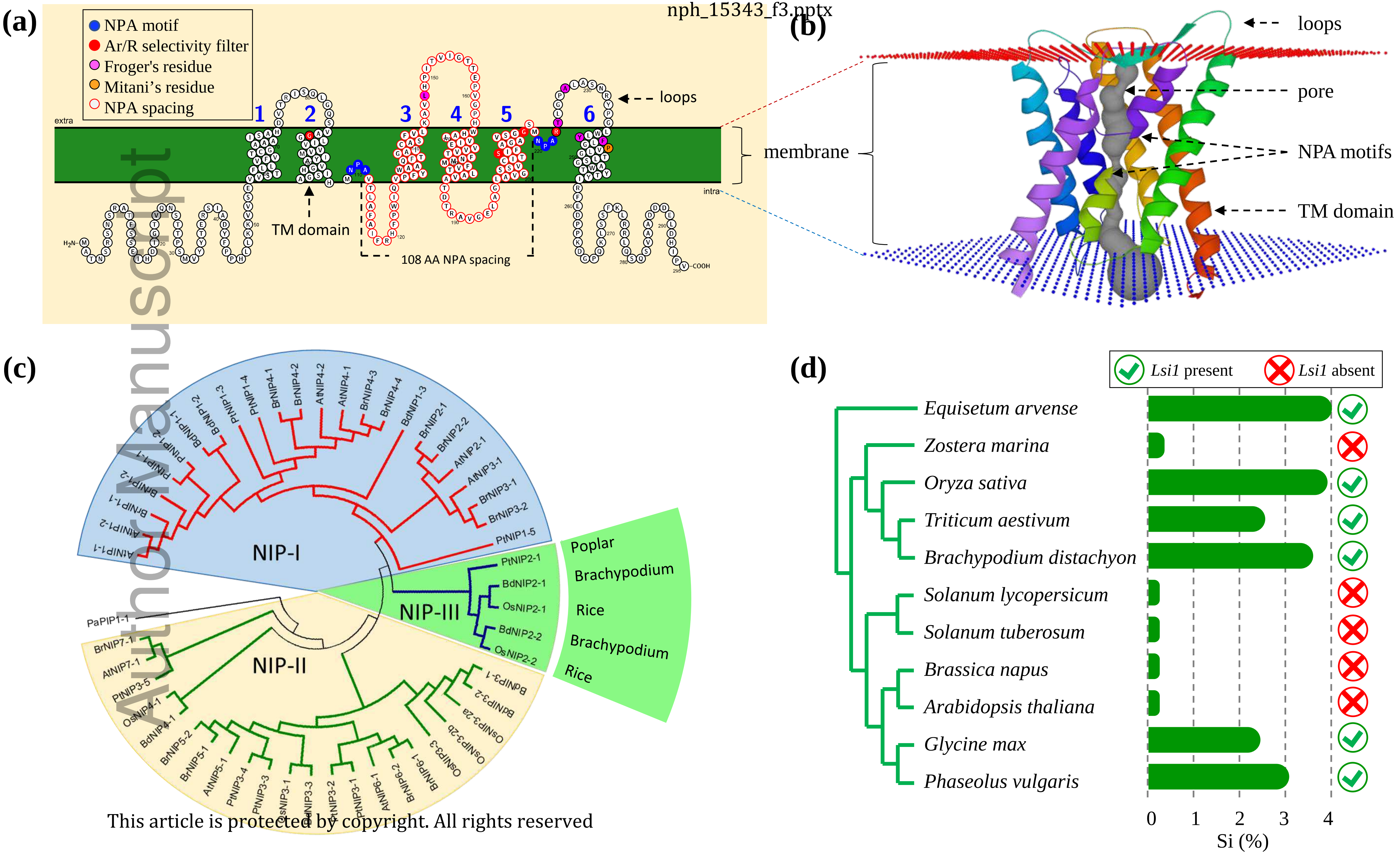
2
3
4
5
6
loops
TM domain
108 AA NPA spacing
H_2N
COOH
(b)
loops
pore
membrane
NPA motifs
TM domain
(c)
NIP-I
NIP-II
NIP-III
AtNIP1-1
AtNIP1-2
BrNIP1-1
BrNIP1-2
PtNIP1-1
PtNIP1-2
BdNIP1-1
BdNIP1-2
PtNIP1-3
PtNIP1-4
BrNIP4-1
BrNIP4-2
AtNIP4-2
AtNIP4-1
BrNIP4-3
BrNIP4-4
BdNIP1-3
BrNIP2-1
BrNIP2-2
AtNIP2-1
AtNIP3-1
BrNIP3-1
BrNIP3-2
PtNIP1-5
PtNIP2-1
BdNIP2-1
OsNIP2-1
BdNIP2-2
OsNIP2-2
Poplar
Brachypodium
Rice
Brachypodium
Rice
PaPIP1-1
BrNIP7-1
AtNIP7-1
PtNIP3-5
OsNIP4-1
BdNIP4-1
BrNIP5-2
BrNIP5-1
AtNIP5-1
PtNIP3-4
PtNIP3-3
OsNIP3-1
BdNIP3-3
PtNIP3-2
PtNIP3-1
AtNIP6-1
BrNIP6-2
BrNIP6-1
OsNIP3-3
OsNIP3-2b
OsNIP3-2a
BdNIP3-2
BdNIP3-1
(d)
✓ *Lsi1* present
✗ *Lsi1* absent
Equisetum arvense
Zostera marina
Oryza sativa
Triticum aestivum
Brachypodium distachyon
Solanum lycopersicum
Solanum tuberosum
Brassica napus
Arabidopsis thaliana
Glycine max
Phaseolus vulgaris
0
1
2
3
4
Si (%)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● NPA motif
● Ar/R selectivity filter
● Froger's residue
● Mitani's residue
○ NPA spacing
extra
intra
1
2
3
4
5
6
loops
TM domain
108 AA NPA spacing
H₂N-
-COOH
(b)
loops
pore
membrane
NPA motifs
TM domain
(c)
NIP-I
NIP-II
NIP-III
AtNIP1-1
BrNIP1-2
BrNIP1-1
BrNIP1-2
PtNIP1-1
PtNIP1-2
BdNIP1-1
BdNIP1-2
PtNIP1-3
PtNIP1-4
BrNIP4-1
BrNIP4-2
AtNIP4-2
AtNIP4-1
BrNIP4-3
BrNIP4-4
BdNIP1-3
BrNIP2-1
BrNIP2-2
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AtNIP3-1
BrNIP3-1
BrNIP3-2
PtNIP1-5
PtNIP2-1
BdNIP2-1
OsNIP2-1
BdNIP2-2
OsNIP2-2
Poplar
Brachypodium
Rice
Brachypodium
Rice
PaPIP1-1
BrNIP7-1
AtNIP7-1
PtNIP3-5
OsNIP4-1
BdNIP4-1
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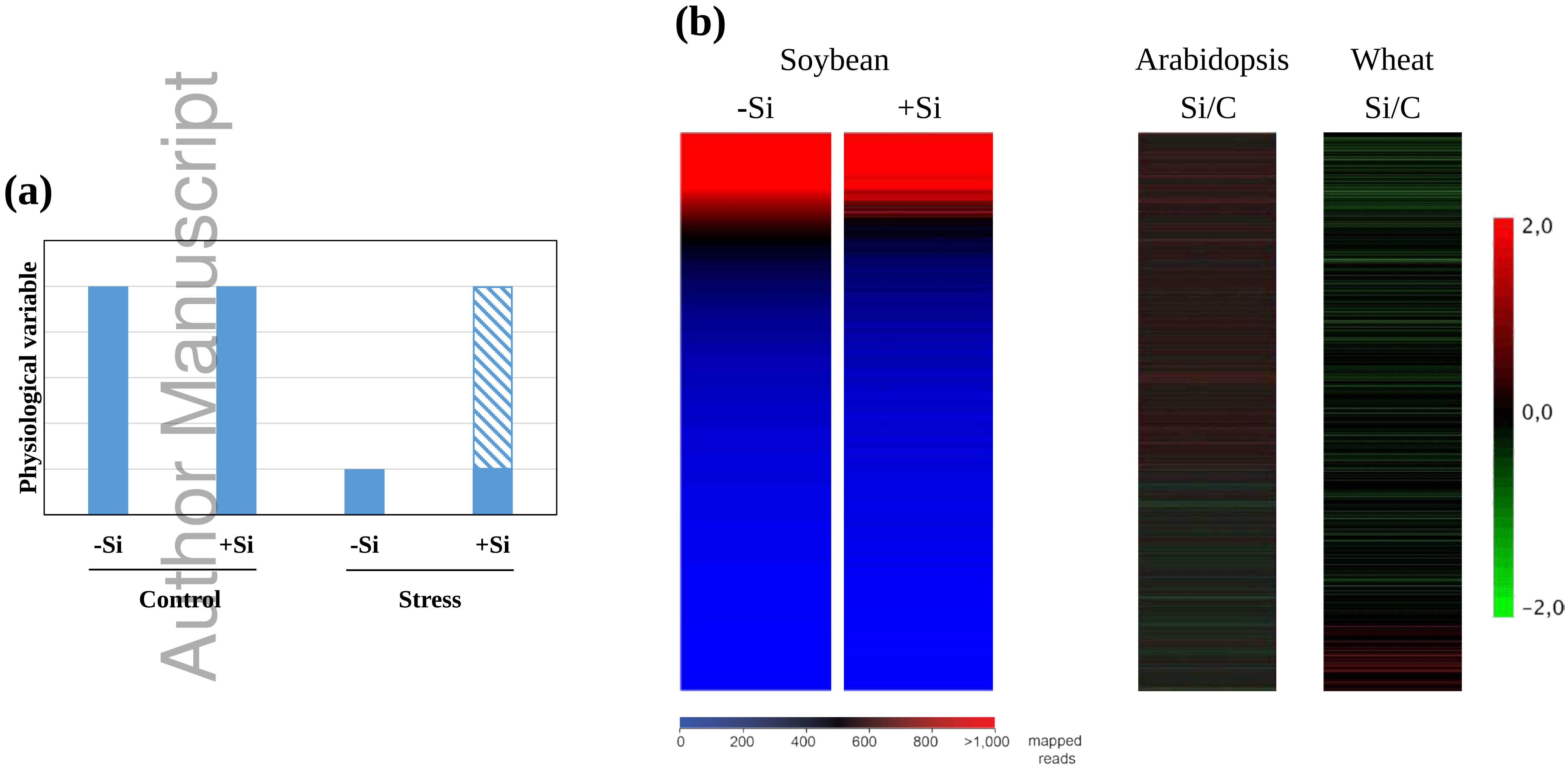
BrNIP5-1
AtNIP5-1
PtNIP3-4
PtNIP3-3
OsNIP3-1
BdNIP3-3
PtNIP3-2
PtNIP3-1
AtNIP6-1
BrNIP6-2
BrNIP6-1
OsNIP3-3
OsNIP3-2b
OsNIP3-2a
BdNIP3-2
BdNIP3-1
(d)
Lsi1 present
Lsi1 absent
Equisetum arvense
Zostera marina
Oryza sativa
Triticum aestivum
Brachypodium distachyon
Solanum lycopersicum
Solanum tuberosum
Brassica napus
Arabidopsis thaliana
Glycine max
Phaseolus vulgaris
0
1
2
3
4
Si (%)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Physiological variable
-Si
+Si
-Si
+Si
Control
Stress
(b)
Soybean
-Si
+Si
Arabidopsis
Si/C
Wheat
Si/C
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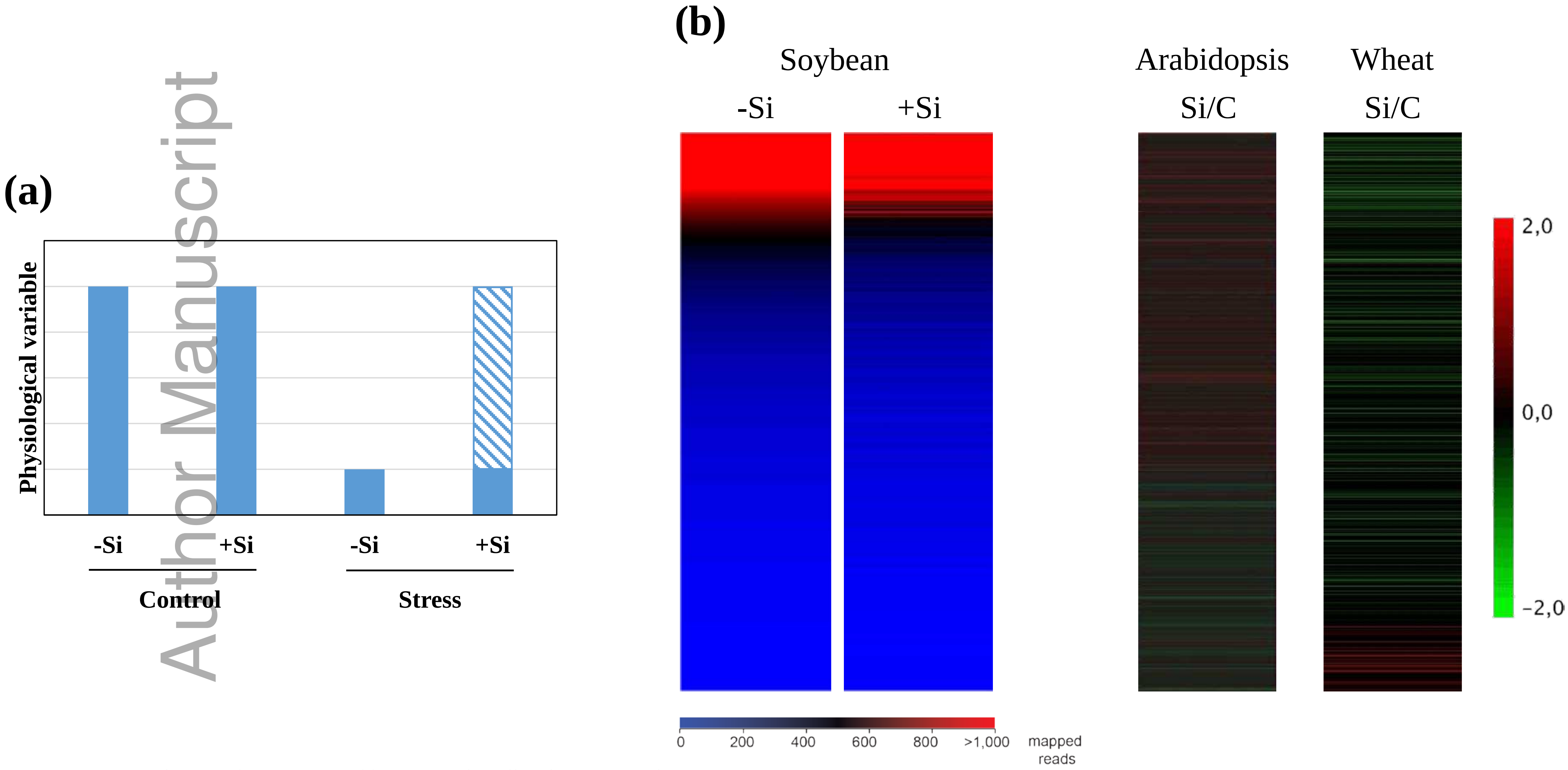
0,0
−2,0
0
200
400
600
800
>1,000
mapped reads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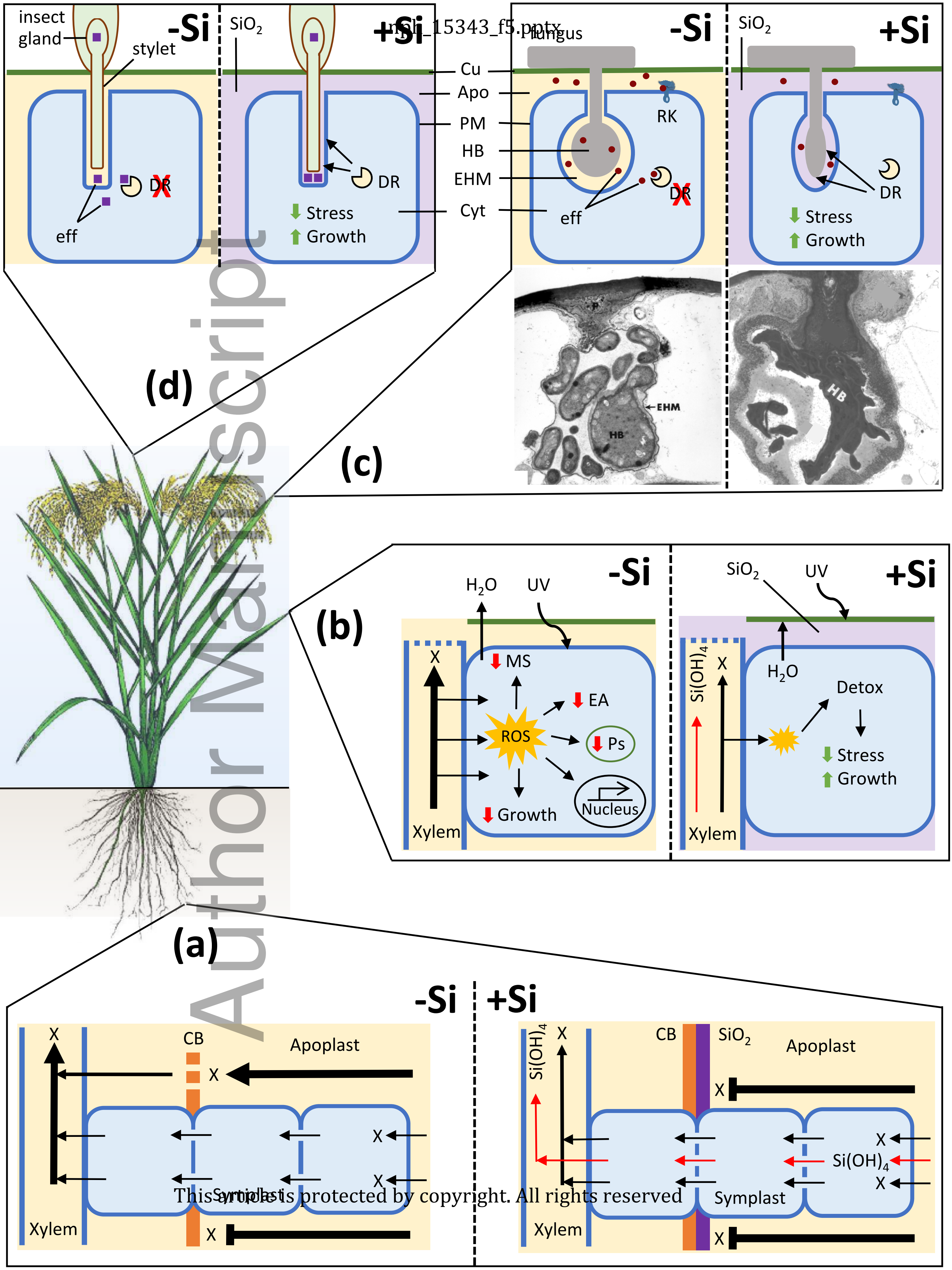
Physiological variable
-Si
+Si
-Si
+Si
Control
Stress
(b)
Soybean
-Si
+Si
Arabidopsis
Si/C
Wheat
Si/C
2,0
0,0
−2,0
0
200
400
600
800
>1,000
mapped reads


(d)
insect gland
stylet
-Si
SiO_2
+Si
eff
DR
X
Stress
Growth
(c)
Fungus
-Si
SiO_2
+Si
Cu
Apo
PM
HB
EHM
Cyt
RK
eff
DR
X
Stress
Growth
EHM
HB
HB
(b)
-Si
H_2O
UV
X
MS
EA
ROS
Ps
Growth
Nucleus
Xylem
+Si
SiO_2
UV
$Si(OH)_4$
X
H_2O
Detox
Stress
Growth
Xylem
(a)
-Si
X
CB
Apoplast
X
X
X
X
Symplast
Xylem
+Si
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X
CB
SiO_2
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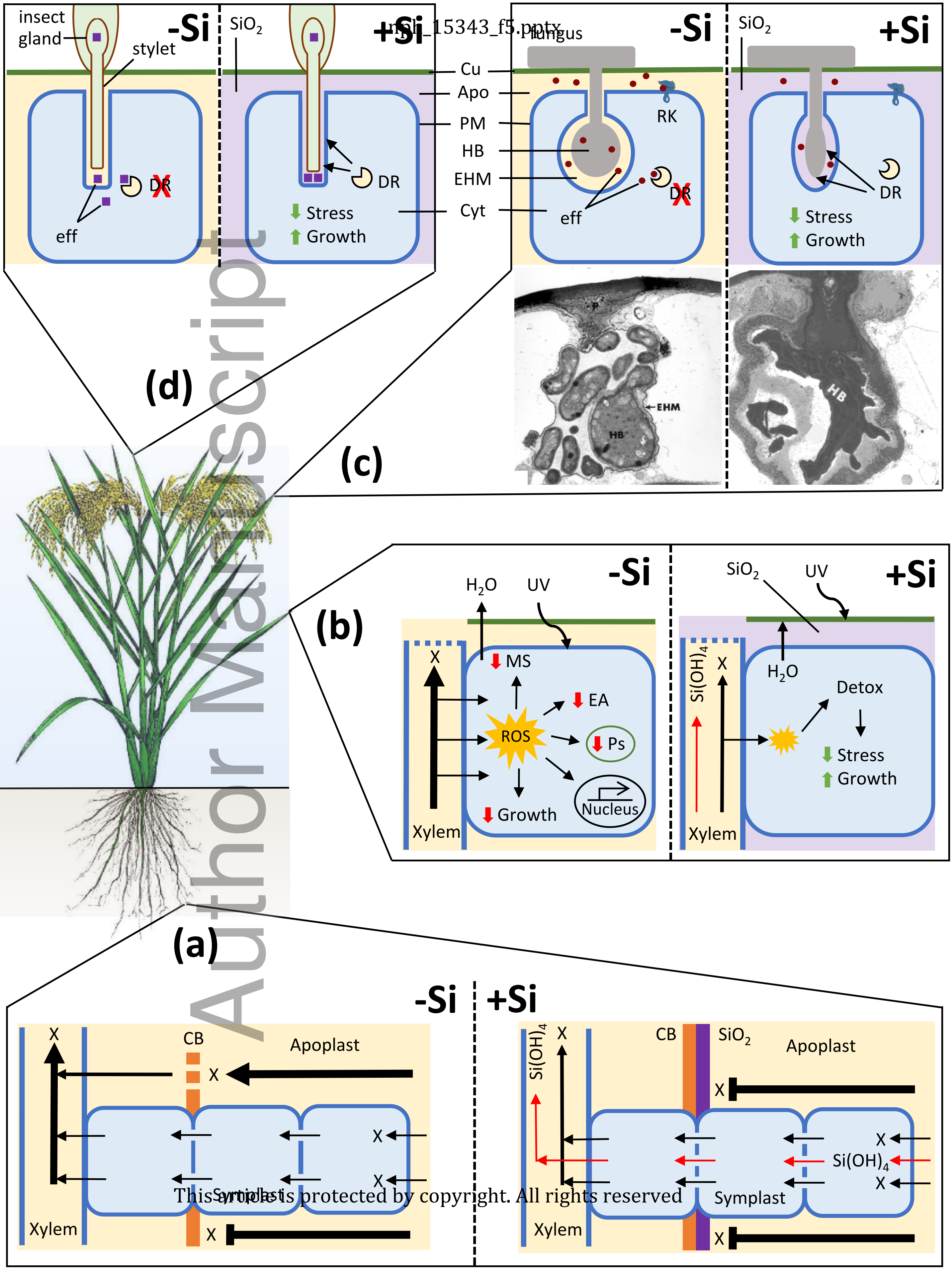
X
X
$Si(OH)_4$
X
Symplast
Xylem
X


insect
gland
stylet
-Si
SiO_2
+Si
eff
DR
DR
Stress
Growth
Fungus
-Si
SiO_2
+Si
Cu
Apo
PM
HB
EHM
Cyt
RK
eff
DR
DR
Stress
Growth
EHM
HB
HB
(d)
(c)
(b)
-Si
H_2O
UV
X
MS
EA
ROS
Ps
Nucleus
Growth
Xylem
+Si
SiO_2
UV
$Si(OH)_4$
X
H_2O
Detox
Stress
Growth
Xylem
(a)
-Si
+Si
X
CB
Apoplast
X
X
X
Symplast
Xylem
X
$Si(OH)_4$
X
CB
SiO_2
Apoplast
X
X
$Si(OH)_4$
X
Symplast
Xylem
X