



Some thoughts on silicon and carbon trade-offs in plants

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Abstract

In 1983, Raven suggested that silica could substitute for lignin or cellulose as a structural material in plants, and should be favoured because of its lower energetic costs. He then asked the question why more plants did not use silica for structural support. Raven's idea eventually led to a whole series of investigations into the substitution of silicon for carbon in plants, so-called trade-offs. In this Opinion we offer some, hopefully helpful, thoughts on this research, and we attempt to answer Raven's question. We conclude that more focus on the distribution of silicon and carbon at the cellular level is needed, and that we should be more careful to avoid teleological thinking.

Keywords Carbon · Phytolith · Silicon · Substitution

Introduction

The Special Issue within which this Opinion Paper is published focusses on the interface between silicon (Si) in the soil and Si in the plant, particularly through

uptake and availability at the root-soil interface. We therefore thought it appropriate to put down some thoughts and ideas on that interfacial question of the interaction between carbon (C) and Si themselves.

It has been said in many soil and plant nutrition university classes the world over that Si is to soil what C is to life. Both form the major element in their respective spheres, and both predominantly form scaffolds around which the basic chemical and biochemical reactions that they are known for can be undertaken in complex and varied environments. The comparisons even extend in numerical directions. Both form fundamentally tetravalent bonds (with a preference for oxygen), both make up approximately 40% of the mass by weight and both often make up a 0.5–5.0% 'occlusion' in the other. So what exactly is the relationship between this silicosphere and the biosphere at a macro-level?

Recent research has focussed on the potential for plants to substitute, or trade-off, Si for C as a more energetically efficient element to place in structural elements of plants, and we will discuss this at length in this Opinion Paper. The secondary questions associated with this include the relative absence of organo-silicon compounds in nature and whether 'substitution' of C by Si is a reasonable concept.

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Raven's idea and his question

In one of the classic reviews of Si in plant biology, Raven (1983) covered a very wide range of material, but it was his section on, 'The energetic costs of SiO₂ relative to those of other structural materials', that has possibly proved the most important, and that concerns us here. There he calculated that on a volume basis using lignin as a structural material requires 20 times

more energy than SiO_2 , while polysaccharide requires 10 times more energy. He then went on to ask why more use was not made of SiO_2 in the plants living today. We will come back to attempt some answers to this question later in this Paper. After Raven (1983) was published it took some years before there was much interest in the idea that SiO_2 could in some way substitute for lignin or cellulose as a structural material in plants, because of its lower energetic costs. But in the last twelve years this has changed and it is now a popular research topic. Here we will first survey the relevant literature and then offer a few insights which may be helpful in moving the area on.

Investigating silicon and carbon trade-offs

The paper that reignited interest in this topic was that by Schoelynck et al. (2010). They investigated silica, lignin and cellulose concentrations in wetland plants and aquatic macrophytes. For aquatic species, higher Si concentrations were correlated with lower cellulose concentrations, but with wetland species, the opposite was found, as cellulose increased with higher Si concentration. For wetland species, lower lignin concentrations were associated with increasing Si concentrations. The authors related these trends to the environments in which aquatic and wetland plants live. Aquatic plants are supported by water, but need to be flexible or they will be damaged in running water. Wetland plants do not have water to support them, and need to be stiff and resistant to predation. It may also be that aquatic vascular plants have less grazers and pathogens to contend with than terrestrial vascular plants (Vermeij, 2016). Following on from Schoelynck et al. (2010), a number of groups have investigated the relationship between Si and various C compounds in plant systems. Here we will not aim to cover all of these papers, but rather give a representative sample.

Schaller et al. (2012a) took a different approach, looking at just one species, *Phragmites australis* (Cav.) Trin. ex Steud., and the effects of increasing Si supply on shoot Si, cellulose and lignin concentrations. In general the culms had higher cellulose/Si and lignin/Si ratios than the leaves, and these ratios decreased with higher Si availability in the substrate. The conclusion was that Si affects both cellulose and phenol metabolism, and that there is a trade-off

between productivity (in leaves) and stabilization (in culms).

The composition of rice straw from across South-East Asia was investigated by Klotzbücher et al. (2018). They found that straw Si concentrations were negatively correlated with both carbon and lignin-derived phenols. It was postulated that lower lignin concentrations in straw with high Si concentrations may explain why it decomposes more quickly. The authors also pointed out that this could be an important factor in C cycling in grasslands.

The idea that there is a trade-off between leaf Si concentration and carbon-based compounds was extended to include defence against insects by Cooke and Leishman (2012). They investigated plant communities from West Head in Ku-ring-gai Chase National Park in Australia. Leaf Si was negatively correlated with concentrations of C, total phenols and tannins. It was also negatively correlated with the abundance of Coleoptera, but not with the other invertebrate groups measured. This suggested that Si might be a better defence against chewing insects than other groups.

The trade-off between leaf Si and phenolic defences was investigated along a two million year chronosequence at Jurien Bay in Western Australia by de Tombeur et al. (2021). They found that the species growing on older, nutrient-poor, soils tended to have high silica concentrations while those species growing on younger soils accumulated more phenolic compounds. The authors considered that using silica as a defence mechanism made sense on the oldest soils as it would use less energy. This energy could then be used for other processes, like reproduction.

The effects of future rises in atmospheric carbon dioxide (+240 ppm) and temperature (+4 °C) were investigated in eight grass species by Johnson and Hartley (2018). Elevated carbon dioxide (+240 ppm) increased phenolic concentrations by 11%, but silicon concentration declined by 12%. The authors suggest that decreased Si under higher atmospheric carbon dioxide concentrations in the future could mean that some grasses will be more palatable to herbivores.

This work has now included investigations into elemental stoichiometry that go beyond Si and C and include elements such as nitrogen and phosphorus (e.g. Schaller et al., 2012b, 2016; Xia et al., 2020). An extensive review of grassland trade-offs between Si% and C% as affected by variable nutrition and water

availability was undertaken by Quigley et al. (2020). They investigated what they refer to as the ‘stoichiometric dilution effect’, whereby elemental compositions must sum to 1, and therefore a fall in one element will result in a rise in others. They reported that Si and C do not follow standard stoichiometric principles, and that trade-off between Si and C occurs to a greater extent in arid conditions. Authors have frequently observed negative relationships between Si and C or lignin. Relationships between other elements are complex, and are beyond the scope of this paper.

Silicon and carbon trade-offs at the cellular level

As we have seen above, there is now a reasonable body of literature that has considered the substitution of C by Si in plants in a whole variety of contexts. Often this concerns mechanical strengthening of the plants, but sometimes defence against predation may also be invoked. But what does this mean at the cellular level? In higher plants there are essentially two types of silica deposition, that which is deposited on a carbohydrate matrix in the cell wall, and that which is deposited elsewhere (often in the cell lumen).

Figure 1 is a schematic diagram, adapted from Hodson (2019a), emphasising the different distributions of C compounds and Si in phytoliths developing along five pathways. In Fig. 1a the primary cell wall (mainly cellulose) becomes silicified, but the protoplast remains intact. Here Si is deposited within a carbohydrate matrix. Secondary cell walls develop to almost fill the lumen in Fig. 1b, and in some cases Si is later deposited on to secondary walls. Lignification is common in secondary cell walls. The third sequence (Fig. 1c), is that envisaged by Kumar et al. (2017), who studied the development of silica cells in sorghum leaves, and found that the deposits developed in the apoplastic space between the primary cell wall and the protoplast. In this case, we would not expect the resulting phytoliths to have a high C content, and cellulose and lignin will certainly be absent. In Fig. 1d the protoplast breaks down, and Si is deposited in the cell lumen. In this case some organelles and membranes, and their breakdown products become entrapped within the phytolith. This type of Si deposition is the most likely to include proteins, lipids and nucleic acids. Finally in Fig. 1e we see a combination of the developmental sequences in

Fig. 1a and d, leading to silica deposition in both the primary cell wall and the lumen. The schematic diagram shown in Fig. 1 is not intended to cover all possible types of phytolith development, but it probably shows the most significant types, and helps to visualise where C compounds and Si are located at the cellular level.

The C content of cell wall and lumen phytoliths differs, as we would expect (Parr and Sullivan, 2014; Hodson, 2019a). There is not much data available, but it appears that the C concentration of lumen deposits varies from 0.1 to 0.5%, while the equivalent figures for cell wall phytoliths are much greater at 3.4 up to a high of 25%. When all of the investigations considered above have analysed total Si in leaves or other organs they are actually including two very different Si pools with very different C contents. Moreover lignin and cellulose will only be found in cell wall phytoliths (Fig. 1a, b and e). We presume that when researchers have considered substitution of C, cellulose or lignin with Si they were thinking about the situation in the cell wall, but what they are including in their analyses is not just cell walls. To add to this complexity lumen deposits (Fig. 1c, d and e) are much more common in grasses and cereals than in any other group of plants. So, for example, when Schoelynck et al. (2010) analysed both grasses and dicots among their wetland species, the analyses for the grasses will have included lumen phytoliths, while the dicot analyses will probably just include cell wall types. Of course, it is quite possible that lumen deposits will contribute to the strengthening of grass tissues, but it is likely that the biomechanics will be different from the cell wall deposits. Many of the investigations that have looked at C and Si trade-offs have concerned grasses and cereals, at least in part. The thinking outlined above does not mean that this work is wrong, but it does complicate interpretation. As Hodson (2019a) noted, we do not know the relative size of the lumen and cell wall phytolith pools in any organ or species, and that is an important topic for future work. It is also possible, even likely, that the ratio between lumen and cell wall types varies with the environmental conditions and over time.

What are we measuring? As we have seen above there are some problems with using whole tissue analyses for Si, C and various organic components to look at trade-offs, and we need to investigate these a little more closely. When discussing cell wall phytoliths,

Carbon and Silicon in Plant Cells

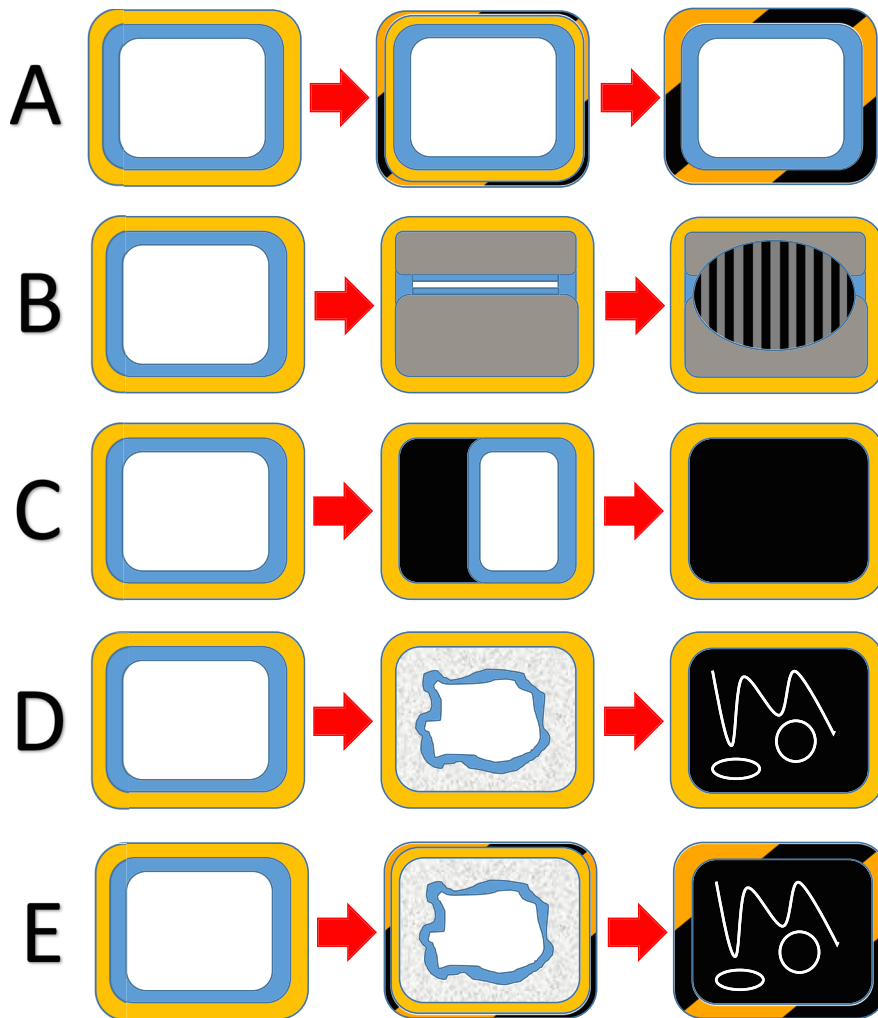


Fig. 1 Carbon and Silicon in Plant Cells. A schematic diagram showing five potential pathways of phytolith development, emphasising the different distributions of carbon compounds and silicon in each case. All begin with the unsilicified cell on the left. **a)** The primary cell wall (mainly cellulose) is silicified, but the protoplast remains intact. **b)** Secondary cell walls (often lignified) develop to almost fill the lumen, and in some cases silica is then deposited on to secondary walls. **c)** Silica is deposited in the space between the primary cell wall and the protoplast, and eventually this fills the lumen. **d)** The protoplast breaks down, and silica is subsequently deposited

within the lumen, entrapping some organelles and membranes (and hence proteins, lipids and possibly nucleic acids). **e)** This is a combination of the developmental sequences in A and D, leading to silica deposition in both the primary cell wall and the lumen. Key: primary cell wall (yellow); cytoplasm (blue); vacuole (white); silica (black); secondary cell wall (grey); silicified primary cell wall (yellow and black diagonal stripes); silicified secondary cell wall (grey and black vertical stripes). Diagram adapted from Hodson (2019a) where more details can be found concerning phytolith development

Hodson (2019a) considered that, ‘If the percentage carbon is high then percentage silicon must be low and vice versa.’ In other words, on a volume or weight basis if one component increases in value the

other must, as a consequence, decrease. In a similar vein, Schoelynck et al. (2010) noted, ‘increased content of one component automatically decreases the relative importance of other components.’ But the key

difference is that Schoelynck et al. used whole plant organ analyses, as have almost all researchers on this topic, and were not directly analysing individual cell walls or phytoliths. Can we use the same thinking for both types of analysis? In this respect, the work of Yamanaka et al. (2012) on silica and lignin distribution in horsetail (*Equisetum hyemale* L.) and their influence on the mechanical properties of the shoot is relevant. They found that silica is deposited only in the epidermis of the internodes, and histochemical analysis showed that lignin was not present in this layer, but in the vascular bundles. They then designed a model structure of a horsetail, and applied a mechanical force to it at right angles to the long axis. The authors could then calculate the response to this force using a finite element method. From this analysis they showed that the silica in the epidermis had a major structural role. Lignin was not involved in structural support, and the authors suggested that it was used in waterproofing the vascular bundle. So can we assume that all, or indeed any, lignin in an organ of any plant species is providing structural support? Again we are not saying that using whole organ analysis is intrinsically wrong, but we do need to be aware of its limitations.

The language of substitution

The language of substitution, even energetically, of Si for C should come with a number of caveats. The first of these is that substitution refers to substitution of function, not substitution of element. Recent research has demonstrated that with ‘directed evolution’ organo-silicon compounds can be enzymatically produced (Kan et al., 2016). However, the requirement for ‘directed evolution’ reflects the absence of naturally occurring organo-silicon compounds. Carbon being displaced directly, substituted as it were, is therefore mechanistically problematic. Nature has not developed enzymes that are able to switch between Si and C as if they are similarly shaped bricks with one being ‘cheaper’ than the other.

A fascinating recent paper by Minden et al. (2021) explored the question of whether trade-offs between Si and C are observed under conditions of nutrient stress, specifically N and P limitation. The overall conclusion of the manuscript was that plants take up more Si under nutrient stress, and that there is

an accompanying decrease in C. The authors imply that as the cost of C accumulation increases as N and P availability decreases, plants shift to a strategy that substitutes Si for C. It is well argued. However, another possible interpretation of the same data is that as nutrient stress decreases C assimilation, continued normal Si uptake (either passively or actively) results in a relative increase in Si over C. Silicon increased greater than C decreased, so however the substitution is mechanistically effected, it is unlikely to be elemental, 1:1 replacement. The seeming replacement of C with Si is perhaps nothing more than dilution of existing C in the plant by mass, with an unaffected and continuing Si uptake. Quigley et al. (2020) provides evidence in grasses that the relative increase in Si over C varies more widely than would be expected by standard stoichiometric relationships as observed with other macronutrients. They conclude that, at least in grasses, trade-off between Si and C accumulation is more than a ‘stoichiometric dilution effect’ and in line with Minden et al.’s study suggest a deliberate strategy to shift to higher Si as C assimilation/availability becomes more challenged.

What do authors precisely mean when the language of substitution is being used? Or, for that matter, when leaves are described as ‘biosilicified’ structures (Wang et al. 2005) is that intended to convey a hybrid, substituted C-Si bonded structure, or are they simply referring to the deposition, perhaps around a C cytoskeleton, of polymerised Si deposits. Plants are not truly substituting Si for C, but Si is intruding and surrounding C structures in cell walls (Fig. 1a, b and e) and solidifying as Si–Si bonds.

Similarly, the language of substitution ‘strategies’ under nutrient or light stress implies that plants have genetically adapted processes that detect C or nutrient limitations, and actively pursue an energetically cheaper end goal for survival. The authors of this Opinion Paper independently came to the conclusion that some of this thinking has come close to teleology. The Collins English Dictionary (1991) defines teleology as, ‘the belief that certain phenomena are best explained in terms of purpose rather than cause.’ We see no purposeful Si uptake, but advantage accruing when Si uptake continues under stressed conditions whatever the limitation may be. The apparent substitution is inadvertent rather than deliberate, and to call it a strategy, in a similar way to mycorrhizal infection for example, is stretching the language

beyond what it can bear. We are not the first to consider this idea, and Harper (1982) stated that, ‘The term “strategy” sounds like a teleology- as if the organism has a planned campaign of behaviour aimed at the future.’ None of us are immune to teleological thinking, and as authors we ourselves have fallen into it at times. But it is something that we should all be guarding against.

Answering Raven’s question

Finally, after nearly 40 years of plant Si research, can we answer the question posed by Raven in 1983? Why are relatively few plants using Si as a structural material?

Firstly, Raven observed that Si was not infrequently depleted in aquatic environments, and that this could limit the growth of organisms such as diatoms, but he did not think limitation was likely for land plants in terrestrial environments. Forty years on, Si limitation now seems unlikely in most natural terrestrial environments, but there is growing evidence that some agricultural systems may have sub-optimal amounts of available Si in their soils (Vandevenne et al., 2012; Hodson, 2019b). However, for most of the history of land plants they have not been under cultivation, so it is difficult to see how Si limitation in the soil could have led to the selection of plants that did not use silica as a structural support.

The second problem Raven suggested was that even if SiO₂ was as effective as lignin, its extra mass might mean that a plant would need additional compression resistant material lower down the shoot. The idea that it is the additional weight of silica that is the problem has received some backing. In the Carboniferous period the Equisetales, ancient horsetails, reached a height of 30 m. Yamanaka et al. (2012) consider that horizontal branching for such plants would be impossible as the branches would be too heavy. So when trees evolved that used lignin as their strengthening agent, they could branch and that gave them a competitive advantage over the Equisetales. Most of the modern day horsetails are modest in size, but the giant horsetails of the tropics can reach 9 m. For comparison the tallest coastal redwood tree is 115 m tall. So at least within the trees there is a fairly compelling reason why high Si accumulation is not found.

Thirdly, Raven wondered whether there was some sort of intrinsic problem in using silica as a structural component. This is difficult to determine, and very many species do use silica, so it does not seem likely.

Raven’s final idea was that saturated Si(OH)₄ solutions in the apoplast might be toxic to plants, but even in 1983 he felt this was unlikely. In the last forty years we have seen many examples of work where apoplastic Si is an advantage to plants (Coskun et al., 2019).

One relatively new idea was not thought of when Raven wrote his review. It is now recognised that the Poales, which are heavy Si accumulators, evolved in the Miocene when atmospheric CO₂ concentration was low. Silica accumulation would mean the plants were better defended when carbon was in short supply (Cooke and Leishman, 2011; Strömberg et al., 2016). Now the CO₂ concentration is higher the Poales are ‘locked in’ to high Si accumulation. In other words a feature that evolved under one set of conditions has been conserved even after the original conditions that provided the selection pressure have been removed.

Conclusion

So in conclusion, even after forty years we are not in a position to totally answer Raven’s question. For trees it does seem that lignin has the advantage because it is lighter than SiO₂. But we do not have a clear idea why most of the herbaceous dicots and non-commelinid monocots are low Si accumulators. However, Raven’s original idea did eventually set in train a whole series of investigations that considered substitution of organic components by Si for structural and defence purposes in plants. Almost all of this work has used whole organ analyses for Si, carbon, lignin and cellulose. There is nothing wrong in doing this, but it is a ‘blunt instrument’, and we would urge future researchers to think more carefully about what is happening at the cellular level. We also consider that we need to be a little more careful in our use of language in this area, as it is easy to fall into a teleological way of thinking.

Author’s contributions MJH and CNG both wrote sections of the text, and both agreed with the final version submitted.

Declarations

Conflict of interest Authors have no conflict of interest to declare.

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