
Benefits of soil phylolith content on the resistance to a combine temperature elevation and water stress of a high silicon accumulating plant (*Oryza Sativa* L.) growing in silicon depleted soil

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CO-PROMOTEURS: PR. J.T. CORNELIS ET IR F. DE TOMBEUR

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Abstract

Global climate change is expected to increase the intensity and the frequency of concurrent stresses. Among them, the sum of the elevation in temperature and the lack of water may have a catastrophic impact on anthropised and natural ecosystems. Silicon (Si) has recently shown some interesting prospects for its effect on the ability of plants to overcome this type of stress. All plants accumulate this element, which is the second most present in the earth's crust, and return it in the form of amorphous crystals called phytoliths (PhSi). This return helps to supply the dissolved Si pool in the soil and contributes to the subsequent intake, especially in highly weathered soils. A pot experiment involving two culture chambers was set up to simulate the impact of the return of PhSi on the growth of rice plants (*Oryza sativa*) under optimal and stress conditions. The stress involves a constant rise in temperature of 4 degrees to be consistent with the Representative Concentration Pathway (RCP) 8.5 scenario of the IPCC (2013) and a period of withholding of water of 10 days. The addition of PhSi significantly increased the amount of Si dissolved in the pots and the amount absorbed by plants. Plants subjected to stress conditions have generally achieved to reverse the adverse effects by increasing the number of secondary roots and decreasing their specific leaf area. These two traits were amplified by the addition of Si. The results of this study show that silicon could have a beneficial impact on the ability of plants to overcome the adverse effects of climate change.

Key-words: Silicon, Combined-stresses, Desertification, *Oryza sativa*, drought, temperature

Résumé

Le changement climatique mondial devrait accroître l'intensité et la fréquence des stress simultanés. Parmi eux, la somme de l'élévation de la température et du manque d'eau pourrait avoir un impact dramatique sur les écosystèmes anthropisés et naturels. Le silicium (Si) a récemment montré des perspectives intéressantes pour son effet sur la capacité des plantes à surmonter ce type de stress. Toutes les plantes accumulent cet élément, qui est le deuxième plus présent dans la croûte terrestre, et le restituent sous forme de cristaux amorphes appelés phytolithes (PhSi). Ce retour contribue à enrichir le pool de Si dissous dans le sol et contrôle l'absorption ultérieure, en particulier dans les sols très altérés. Une expérience en pot impliquant deux chambres de culture a été préparée pour simuler l'impact du retour de PhSi sur la croissance des plants de riz (*Oryza sativa*) dans des conditions optimales et de stress. Le stress implique une augmentation constante de la température de 4 degrés pour être cohérent avec le scénario du "Representative Concentration Pathway" (RCP) 8.5 du GIEC (2013) et une période d'arrêt total de l'arrosage de 10 jours. L'ajout de PhSi a significativement augmenté la quantité de Si dissous dans les pots et la quantité absorbée par les plantes. Les plantes soumises à des conditions de stress ont généralement réussi à inverser les effets néfastes en augmentant leur nombre de racines secondaires et en diminuant leur surface foliaire spécifique. Ces deux traits ont été amplifiés par l'ajout de silicium. Les résultats de cette étude montrent que le silicium pourrait avoir un impact bénéfique sur la capacité des plantes à surmonter les effets néfastes du changement climatique.

Mots-clés: Silicium, Stress combiné, Desertification, *Oryza sativa*, Sécheresse, Temperature

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1 GLOBAL CONTEXT

For many years nutrient cycles have received relatively little attention by researchers. After the green revolution, the soil was considered as a black box where the focus was not on cycles but on inputs. This strategy permitted the absorption of the demographic growth and brought an unprecedented "standard of living" for a large part of the population (Pingali, 2012). Food security accompanied by an increase in per capita calorie intake, as well as a shift in the composition of diets (FAO, 2018) acquired in the richest countries have facilitated technological progress, urbanization and trade globalization. However, this economic growth has been uneven across the globe, leaving two billion people having various micronutrient deficiencies and 821 million people suffer from hunger (FAO, 2018). In addition, this "golden age" also addresses the challenges associated with climate change, ecosystems pollution (partially due to the massive use of chemical fertilizers), soil degradation, the increase in inequalities and associated populations movements, eutrophication and loss of biodiversity among others (Pimentel & Pimentel, 1990).

All these consequences of anthropogenic management are related. By ignoring the complexity of the interactions that govern the functioning of soils and therefore of ecosystems, human kind has put ecosystems under pressure (Zdruli *et al.*, 2017). An ecosystem is an interlinked social-ecological system. It constantly undergoes disturbances but it is able, to a certain extent, to maintain its equilibrium thanks to the links which unite all its components, biotic and abiotic, together. This ability is called "resilience" (Peterson *et al.*, 1998; Carpenter *et al.*, 2001). When the links are broken, it makes the other components more vulnerable and reduces its resilience. If the disturbance is substantial, it causes a cascade of reactions and the system shifts to an alternative state (IPCC, 2019) that is certainly less beneficial for humans. The degree and the frequency of anthropogenic disturbances have degraded many ecosystems resilience, leading them to collapse (Berdugo *et al.*, 2020; IPCC, 2019; Cherlet *et al.*, 2018; Nicholson, 1998). The first symptoms of land degradation are erosion, fertility loss, salinization, acidification, compaction, loss of biodiversity and soil carbon content until the complete loss of ecosystem goods (Koch *et al.*, 2013; ISSS, 1996).

Usually, when an ecosystem shows pathogenic signs, it is already too late for men to restore its previous condition (Rapport *et al.*, 1998). According to the world atlas of desertification (2018), over 75% of the Earth's land area is already degraded and over 90% could become degraded by 2050. In 2019, Ibrahim Thiaw, the executive secretary of the United Nations Convention to Combat Desertification (UNCCD), estimated that 3.2 billion people, half of humanity, were already suffering from land degradation. Most of the time, land degradation is caused by the overexploitation of soil, the inefficient use of water, irrigation, deforestation, overgrazing, high temperatures or intense drought (Grainger, 1990; Wynn Owen, 2019; D'odorico *et al.*, 2013).

These issues are expected to be greater in the future alongside global change and demographic explosion, particularly in drylands (Reynolds *et al.*, 2007; Berdugo *et al.*, 2020; Thiaw, 2019; Feng & Fu, 2013; Koch *et al.*, 2013; Kellner *et al.*, 2011; D'odorico *et al.*, 2013). Global drylands, including hyper-arid, arid, semiarid, and dry subhumid areas cover about 41 % of the earth's terrestrial surface and are home to more than a third of the world's population (Feng & Fu, 2013). Land degradation in the drylands has its own name: "desertification". In 2011, the UNEP / FAO / GEF Project "Land Degradation Assessment in Drylands (LADA)" estimated that more than twelve million hectares of arable lands are lost each year and this rate is increasing. The conventional reaction to the loss of fertility is to increase the doses of fertilization, antifungals and herbicides even though these practices have contributed to the weakening of ecosystems around the world (Pimentel & Pimentel, 1990). It also increases the production cost, accelerating the precariousness of farmers. By confusing the causes and the consequences of the problem, no lasting solution is being brought to counter the progression of desertification in the world.

The desertification in the drylands will have catastrophic outcomes as it represents the loss of ecosystem services of 44% of the world's cultivated areas hosting a population at 90% from developing countries who rely on their land for a major part of their incomes (FAO, 2019). However, the occidental countries will directly or indirectly suffer from land desertification as well. By the end of this century, the dryland surface is expected to grow by 10% especially in North America, Australia and the north side of the Mediterranean Sea (Feng & Fu, 2013). For instance, the surface of Spain is at 75% at risk of desertification (Wynn Owen, 2019).

Desertification represents an annual direct hit of 40 billion USD worldwide mainly due to the loss of fertility (Winslow *et al.*, 2004; Kellner *et al.*, 2011). Additionally, the hidden, indirect and non-material costs are incommensurable. The loss of ecosystem goods and services such as water and food security will increase food prices, land grabbing and poverty (IPCC, 2019; UNCCD, 2017). The growing inequalities enhance instabilities, war and migration issues worldwide (D'odorico *et al.*, 2013; UNCCD, 2017). In 2018, the World Atlas of Desertification estimated that the number of people who will be displaced due to land resources scarcity could be up to 10 billion by the end of the century. Moreover, the increase in the use of inputs, the loss of biodiversity and the land degradation itself, directly contribute to accelerate global changes (IPCC, 2019; D'odorico *et al.*, 2013; Huang *et al.*, 2017).

Therefore, urgent actions are needed on a regional scale to improve the management and restoration of drylands and achieve land degradation neutrality (IPCC, 2019). Meaning that research which could contribute to increase the resilience of ecosystems and populations to climate change and to repeated critical conditions associated with drought, high temperatures, pests and diseases are valuable (FAO, 2019).

During the past two decades, research on silicon (Si) has replaced this element as a central component of ecosystems (Nicholson, 1998; Katz, 2019) and revealed remarkable impacts on biotic and abiotic stresses alleviation (Debona *et al.*, 2017), showing interesting prospects about its true role on land sustainability.

Through this work, we tested the potential benefits of Si as an element improving the resilience of ecosystems to drought and temperature elevation stresses to take part in the land degradation neutrality (LDN) goal.

2 INTRODUCTION

2.1 Silicon Cycle

Silicon (Si) is an element of almost all soil parent material and occurs in more than 370 rock forming minerals (Sommer *et al.*, 2006), rendering it the second most abundant element of the Earth's crust (29%), after oxygen (Haynes, 2014; Iler, 1979; Wedepohl, 1995). The chemical weathering of lithogenic silica (LSi) releases Si in soil solution in the form of aqueous monosilicic acid (H_4SiO_4) supplying the dissolved pool (DSi). Inside the soil system, if not absorbed by the biota, monosilicic acid can either be adsorbed on reactive minerals or be mobilised in the formation of phyllosilicates (PSi), i.e. secondary clay minerals. Both processes influence the physicochemical properties of soils (Gieseking, 1949) making the weathering of silicate minerals one of the major driving factor of pedogenesis and soil classification. Weathering depends on the five soil-forming factors² which heterogeneity around the globe causes soil diversity (Cornelis & Delvaux, 2016). Monosilicic acid can also be transferred out of the ground to the hydrosphere and end up in the ocean where diatoms, which compose 50% of the phytoplankton biomass, use it to build their skeleton by consuming CO_2 (Tréguer & Pondaven, 2000). Thus, the process of silicate weathering takes part in the main process of carbon sequestration (i.e. ocean sink) and then in the regulation of atmospheric CO_2 . Eventually, the remaining part of the DSi can be bioavailable for plant uptake and subsequently precipitate in tissues in the form of amorphous silicate particles, called phytolith (PhSi). Once deposited, silicon is not remobilized (Raven, 2001) and will only return to soil through litter fall (Figure 1).

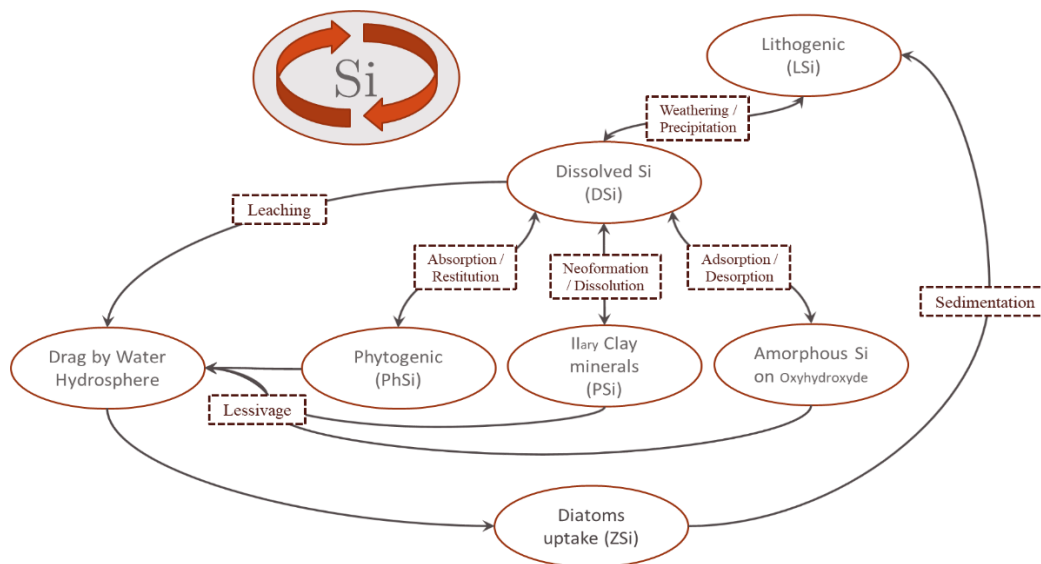


Figure 1: Silicon Cycle

² Parent rock, climate, topography, age and biota (Cornelis & Delvaux, 2016).

2.2 Silicon in plants

Silicon absorption by plants is on growing interest in recent years, due to its contribution to alleviate stresses. Indeed, numerous studies have revealed that plants supplied with Si show a better resistance to abiotic and biotic stresses such as infectious diseases, herbivory, gravity, metal toxicity, high and low temperatures, UV radiation, lodging, nutrient deficiencies and excesses, drought and salinity. In addition, Si uptake is also assumed to enhance growth, yield, crop quality, photosynthesis and N₂ fixation (Guntzer *et al.*, 2011; Rodrigues & Datnoff, 2015; Coskun *et al.*, 2016; Debona *et al.*, 2017).

However, the link between those physiological adaptations and the Si uptake is still controversial (Exley & Guerriero, 2019). Specialists debating on the direct (Debona *et al.*, 2017; Fauteux *et al.*, 2005) or indirect (Coskun *et al.*, 2019; Vivancos *et al.*, 2015) role of Si in the observed physiologic and metabolic changes. Indeed, during the last two decades and due to the lack of knowledge about this element, numerous studies have hypothesised on the mechanistic role of Si inside the plant (e.g. Ghareeb *et al.*, 2011; Bélanger *et al.*, 2003). It has been proven that amorphous Si deposition in plant cells improves rigidity, conferring to the roots, stems and leaves erectness and physical barrier against pollutant, herbivores, and parasites (Ma & Yamaji, 2006; Ma & Yamaji 2008). Additionally, the mechanisms of accumulation and translocation, which were firstly thought to depend only on water flux, have been proven to be the results of active Si transporters (Ma *et al.*, 2006). This important breakthrough, which was quickly followed by similar discoveries on many plants (e.g. Chiba *et al.*, 2009; Mitani *et al.*, 2009; Mitani *et al.*, 2011; Montpetit *et al.*, 2012; Deshmukh *et al.*, 2013; Grégoire *et al.*, 2012; see Ma & Yamaji 2015 for an overview), exacerbates the theories of direct and specific impacts of Si on plants. Besides, it has been observed several times that, beyond a simple role of physical barrier, Si enhances physiological adaptations (Cooke & Leishman, 2016). Assumptions were articulated on hypothetic roles of Si including priming of plant immune responses, alterations in phytohormone homeostasis, amino acid metabolism, regulation of iron homeostasis, silicon-driven photorespiration and interaction with defence signalling components (Detmann *et al.*, 2013; Van Bockhaven *et al.*, 2013). However, none of those prophylactic traits have been proven to be the direct consequence of Si intake, physical barrier proponents claiming that “any observed physiological or metabolic adaptation would have been the result of correlative evidence or indirect effect” (Coskun *et al.*, 2019).

The lack of knowledge on the mechanistic role of Si inside the plant increases the incertitude around its essentiality and its beneficial effects in ordinary conditions (Liang *et al.*, 2015). Consequently, Si is not considered as an essential element for plants (Epstein, 1999), but as “quasi-essential” due to the benefits inherent in its absorption during stressful conditions (Epstein, 2009). This may partly explain why the use of Si has not been established itself in daily agronomic practices around the world. However, either direct or indirect, those benefits may help to reduce the quantity of chemicals inputs (Rodrigues & Datnoff, 2015; Liang *et al.*, 2015; Johnson & Hartley, 2017) in every continent as seven out of the ten most produced crops in the world (ranked by quantity) are Si accumulators³ (Guntzer *et al.*, 2011). Indeed, Si is already used on a regular basis in many countries, especially in Japan where researchers are pioneers on the subject (Rodrigues & Datnoff, 2015).

Additionally, even if there is no general agreement on the benefits inherent to the absorption of Si by plants in non-stressful conditions, its intake could improve overall plant resilience. Increasing the concentration of silicon in the soil has been shown to improve root growth and stomatal conduction by the silification of endodermal tissues (Lux *et al.*, 1999) which helps to maintain high photosynthetic rate when water or temperature stress occurs (Guntzer *et al.*, 2011; Rodrigues & Datnoff, 2015). However, researches have usually focus on the consequences of extreme conditions (IPCC, 2019) but rarely on the effect of small increases in temperature (Peng *et al.*, 2004) nor simultaneous stresses. However several works initiated by Mittler in 2006 have shown that the combination of stresses can no longer be

³ Plants are considered as Si accumulators when Si concentration is greater than 1% dry weight (Epstein 1999).

interpreted as a passive superposition but as a single stress involving a single physiological response. Hence, studying the impact of climate change - which implies an increase in the frequency of concurrent stresses - encompasses studying several stresses simultaneously (Mittler, 2006; Suzuki *et al.*, 2014; Rang *et al.*, 2011; Jagadish *et al.*, 2011). To our knowledge, there is still no experimental studies on the impact of Si for the alleviation of the concurrent elevation of temperature and water stress. As Johnson *et al.* wrote in 2019: “Given the important role played by Si in plant stress alleviation, it is surprising that so little is known about how global warming will affect Si uptake in plants”.

2.3 Silicon depleted soil

Plant Si uptake is driven by the concentration of dissolved Si (DSi) in soils which ranges between 0.1 and 0.6 mM (Epstein, 1994). However, this concentration can vary widely depending on the mineralogy of the soil and the weathering stage. Indeed, young soils are deficient in dissolved Si because silicate minerals are poorly altered due to the alteration of carbonates which consumes protons and because they are strongly adsorbed on secondary minerals when the soil pH is high (de Tombeur *et al.*, 2020a). On the other hand, advanced-stage weathering is associated with the leaching of the LSi and P_{Si} pools because of the acidification and the oxidizing condition in the soil. It has the consequence of concentrating the Si in unalterable crystalline form such as quartz and muscovite (Cornélis & Delvaux, 2016). These crystalline minerals are very stable in soils and poorly contribute to the dissolved pool. Highly weathered soils can therefore contain a lot of Si without it being available to plants. This is called a Si depleted soil. This natural phenomenon is reinforced by the intake of Si by plants, particularly in productive ecosystems and Si accumulating plants such as grasslands (Blecker *et al.*, 2006) or croplands (Makabe *et al.*, 2009). It has been calculated that 210 to 224 million tonnes of Si are removed annually from cultivated soils on a global scale (Matichenkov & Bocharnikova, 2001), which significantly unbalances the biogeochemical cycle of Si in the soil and limits yield and plant growth (McGinnity, 2015). Indeed, along a weathering gradient and the progressive depletion of the LSi and P_{Si} pools, the DSi pool and the readily plant uptake are progressively driven by PhSi returned to soil through litter fall (de Tombeur *et al.*, 2020b). Hence, in Si depleted soils, the quantity of phytolith precipitated in plants tissues exerts a control over the subsequent Si uptake, i.e. the biological Si feedback loop (Cornélis & Delvaux, 2016). Breaking the biogeochemical cycle of Si could weaken the resilience of ecosystems and make them more vulnerable to climate change.

Therefore, this experiment aims to help the understanding on the potential benefits of the Si feedback loop on the ability of a plant to alleviate a combined elevation of temperature and water stress.

2.4 Inclusion of belowground traits

For this purpose, it has been chosen to study belowground traits in addition of the aboveground traits. Belowground traits help the understanding of how the plant is adapting to its environment since the different metabolisms of shoots and roots may respond contrastively to the stressors (Gargallo-Garriga *et al.*, 2014). There is now growing recognition by ecologists that above and belowground trait-based approaches improve the capacity to predict the consequences of environmental changes on plant communities and ecosystems functions and services (Bardgett *et al.*, 2014; Laliberté, 2017). Therefore the interaction between Si and both the roots architecture and the mycorrhizal colonisation have been characterised. Furthermore, the close collaboration with symbiotic fungi is one of the major adaptation of plants to stress resistance (Redman *et al.*, 2011; Rodriguez *et al.*, 2008; Ruiz-Sanchez *et al.*, 2011). However, few studies have been interested in the influence of Si on the relationship between the plant and their symbiotes. Although the coevolution between roots and arbuscular mycorrhizal fungi (AMF) is determinant in both biological weathering (Taylor *et al.*, 2009) and accumulation of Si (Yost & Fox,

1982; Clark & Zeto 1996; Frew *et al.*, 2017), to our knowledge, only one study has revealed a significant impact of Si on AMF colonization (Oye Anda *et al.*, 2016). It showed a modest increase in the presence of arbuscules (but not on vesicles nor hyphae) for banana plants supplied with Si.

2.5 Model plant

Rice (*Oryza Sativa*) has been chosen to be the model plant because it is known as a great Si accumulator - up to 10% of shoot dry weight (Ma *et al.*, 2006) - and to be vulnerable to water scarcity. It is the world most valuable plant (FAOSTAT, 2020) and thus one of the most studied. This is partially due to its short-life-cycle (around 4 months) which allows up to three harvests a year and short time studies. Rice plant symbolises the grassland and the cropland which are the major part (39%) of the drylands surface (FAO, 2019). Those lands have been identified as one of the most vulnerable economic areas to climate change (D'odorico *et al.*, 2013; Cherlet *et al.*, 2018, Huang *et al.*, 2017; Wassmann *et al.*, 2009).

Moreover, rice perfectly represents the danger of the current situation. It is the staple food and major income crop of an estimated 3.5 billion people worldwide mainly in poor and densely populated areas (IRRI, 2002). As the highest population growth rates are in developing countries, rice production has to increase proportionately. Between 1966 and 2000 rice production increased by 130%, 84% of which is attributed to modern farming techniques (Muthayya *et al.*, 2014). This means that a non-negligible part of this increase was made by the appropriation of fertile areas, in particular in irrigated areas. Today, rice accounts for half of the world irrigated lands alone. By 2050, demand will increase by 70% (Muthayya *et al.*, 2014) but there is no longer possibilities of increasing the amount of fertile lands. At the same time, land degradation and climate change are estimated to lead to a reduction of global crop yields by about 10% (Cherlet *et al.*, 2018). This reduction will probably be greater for rice in drylands considering its technical itinerary and its great demand for water. Drought already affects 23 million hectares of Asian rice alone and this area is predicted to double by the end of this century (IRRI, 2002; Jagadish *et al.*, 2011). Heat waves have already provoke dangerous loss of fertility (Peng *et al.*, 2004; Welch *et al.*, 2010). Rice production cannot escape the global consequences of climate change. During all these years, rice production has been an example of mismanagement through the over-exploitation of water and land and through the excessive use of inputs to counter the weakening of monocultures (Pimentel & Pimentel, 1990; Singh, 2000).

3 MATERIAL & METHODS

3.1 Plant material and growth conditions

Rice plants (*Oryza sativa* subsp. Koshihara) were grown from seeds in controlled environment conditions with three degrees of phytolith inputs. This experiment was conducted at the faculty of Gembloux Agro Bio Tech, University of Liège from the 28th of February (sowing day) to the 6th of May (day of harvest). Seeds were pre-germinated for 7 days in deionized water and then stand in tap water for additional 7 days between two layers of filter paper. Four of the better seeds were planted in the centre of each pot and then only the most vigorous seedling was left to grow. To elude the effects of endogenous rhythm in plants (Johanson *et al.*, 1996), all the plants were sowed at the same moment. Two Fitotron® growth chambers (Weiss Gallenkamp Ltd, Loughborough, UK) were monitored continuously throughout the experiment (Figure 2). The first chamber was set on optimal conditions, following the procedure recommended by Kohl (2015): 26/23°C (day/night temperature). Night temperature was 3°C lower than the day temperature according to Harrington (2010). The second chamber was used to simulate the increase in temperature expected in the drylands within this century. The temperature was maintained at 30/27°C, i.e. 4 degrees above the first chamber, to be consistent with the Representative Concentration Pathway (RCP) 8.5 scenario, projecting an additional warming of over 4°C in drylands by the end of the 21st century (IPCC, 2013). Both chambers were maintained on 11 h photoperiod a day, whereas the atmospheric relative humidity was set on 70% for the whole period (Kohl, 2015).



Figure 2: Phytotron, inside view

3.2 Pots composition

All plastic pots (18 × 18 × 23 cm) were filled with 7.5 kg of a substrate composed at 95% of quartz white sand 0-1 mm (Hubo België SA, Wommelgem, Belgique). To ensure anchorage of the mycorrhizal fungi and avoid micro-deficiencies, 5% of the substrate was made of a loamy soil. The soil was collected on February 11, 2020 from a B horizon of a luvisol from the “Grand-Leez” forest in Gembloux, Belgium (4°79'E, 50°59'N, 174m a.s.l.). Following approximately 72 hours of air drying in an oven, the soil was screened through a 2-mm sieve (Figure 3) and mixed to the sand to form the substrate. Three replicates of the substrate were analysed for pH-H₂O, pH-KCl and soluble Si, Iron (Fe) and Aluminium (Al), extracted with CaCl₂. The initial properties were: pH-H₂O 5.2; pH-KCl 4.6; Si 7.43 mg/kg; Fe 0.047 mg/kg and Al 0.082 mg/kg. Then the substrate of each pot was mixed, homogeneously and by hand covered with gloves, with the phytoliths and 600 mg of arbuscular mycorrhizal fungi (AMF)



Figure 3: Screening

powder (Figure 4). The powder is the Inoq Advantage product containing 202 million of *Rhizoglyphus irregulare* propagules per kg of powder (INOQ GmbH, Schnega, Germany).

Phytoliths were incorporated in three rates of 0, 1000 or 2000 mg/kg of dry soil. The upper rate corresponds⁴ to the maximum concentration of the biogenic pool (mainly phytoliths) found in the topsoil of an Australian chronosequence by de Tombeur *et al.* (2020a) and to the stable pool of phytoliths found in rainforest by Alexandre *et al.* (1997). Phytoliths collected from rice hulls were found commercially from the brand GrowSil (SioTex Corp., Austin, USA). The experimental design was a randomized complete block to prevent lateral heterogeneity inside the phytotrons (Figure 5). Each treatment was represented by 7 replicates for a total of 42 pots (21 per chamber).

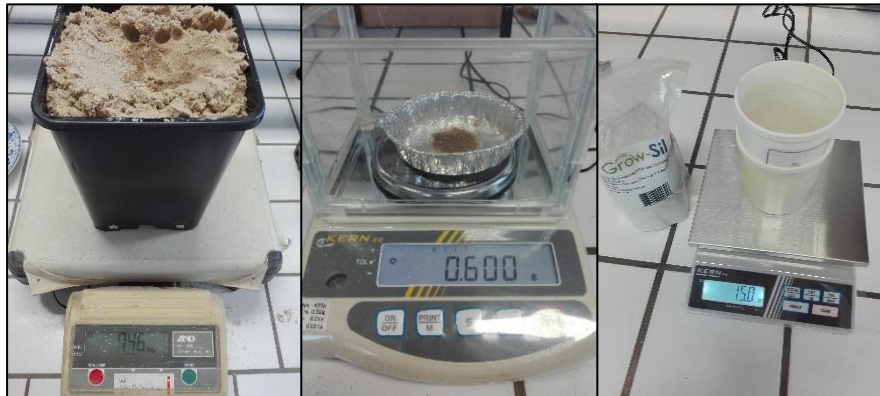


Figure 4: Incorporation of AMF propagules and phytoliths

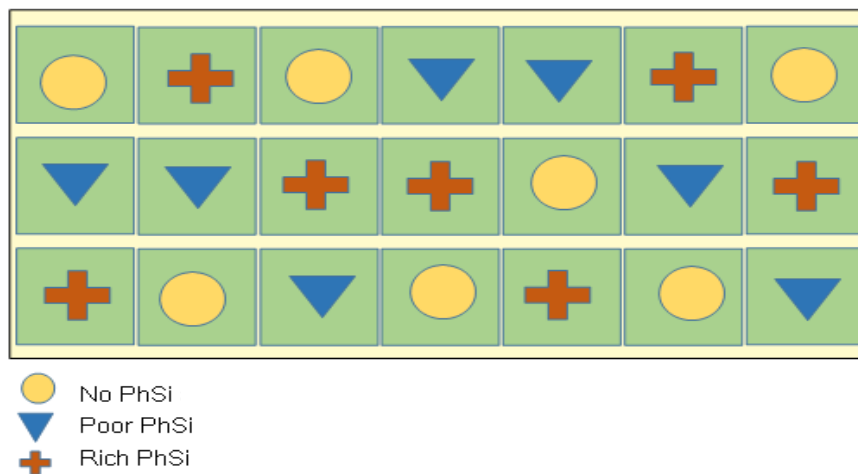


Figure 5: Randomized complete block design

3.3 Water and nutrient regime

Both chambers received sufficient irrigation and nutrients during 24 days after sowing (DAS) corresponding to 200 mL of tap water per pot per day. This amount has been calculated according to the standard of crop water requirement established by the FAO in 1992 (see Annex 2). The nutrient supply was ensured by 10 mL of a high nutritive solution (Hy-Pro Hydro A+B) per liter of irrigation water and was completely stopped for both chambers when the watering frequency was differentiated (see below). Twenty-four DAS, water was flowing increasingly out of the pots. It was thus decided to reduce the

⁴ With a 1500kg/m³ bulk density and 0.23m high pots

number of replicates to 6 per group (see below) and the water regime to 100 mL in both chambers until the end of the experiment. Irrigation frequency remained constant for the optimal chamber, corresponding to a watering every week-day.

On the 22nd of March, in the beginning of the tillering stage, the watering frequency of the hot chamber was reduced by half for 10 days and then by a quarter for 8 more days (see Figure 6) in order to acclimate the plant to the water scarcity, following persona advice from Pr. Hans Lambers. On the 11th of April, 44 DAS, drought stress conditions were imposed in the hot chamber by withholding water for 10 days. Thereafter, the rewatering began on the 22nd of April (i.e. beginning of the panicle initiation) both chambers received the same amount of water (100 mL/pot/day) until the day of harvest.

The experiment has been completed on the 6th of May, 68 DAS. Plants were harvested and analyses were carried out according to the following method.

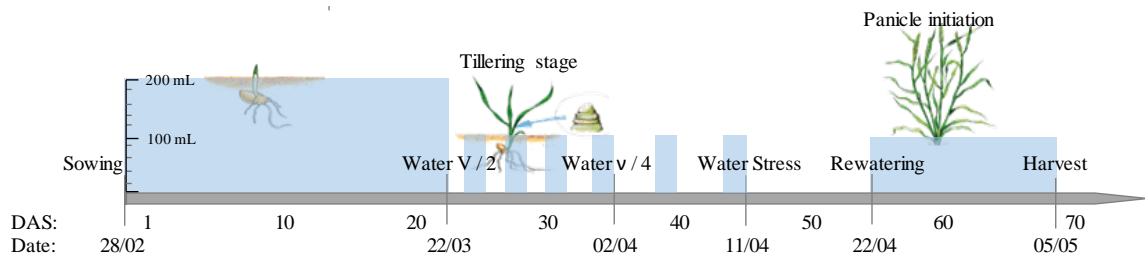


Figure 6: Timeline of water regime in the warm chamber

3.4 Plant sampling and analysis

3.4.1 Shoot

Sixty-eight days after sowing, the base of the stem was cut 1 cm above the soil surface and washed with deionised water to prevent soil contamination. For each plant, the height, the number of leaves, the leaf arc of the third older leaf and the shoot weight were measured. The leaf arc (Figure 7B) characterizes the erectness of the leaves which is a functional trait of plants (Zanao *et al.*, 2010). Then the leaves were separated from the stem, platted and scanned (Figure 7A). The pictures were treated with a computer code on the octave software in order to measure the total leaf area (see Annex 3). Stem and leaves dry mass were weighted after 72 hours in a 40°C oven (Tavakkoli *et al.*, 2011). Total leaf area was divided by the total leaf dry mass to allow the specific leaf area (SLA) calculation. The total water content was calculated following the method described by Jones & Turner (1978).

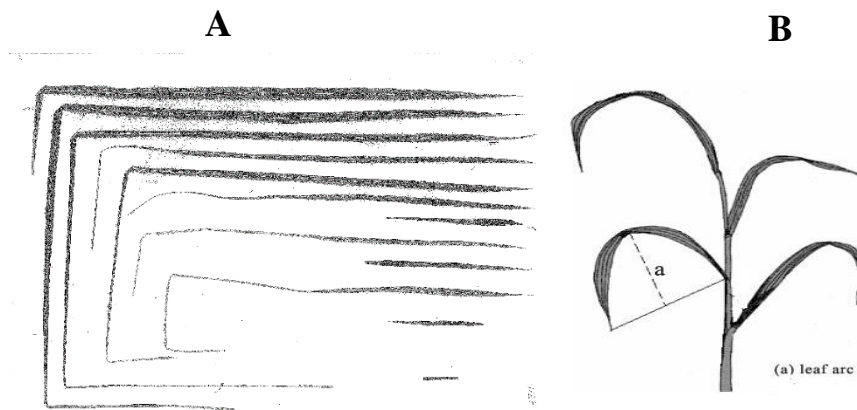


Figure 7: Leaves Trait A: Leaves platted and scanned for surface calculation. B: Measure of the leaf arc (Zanao *et al.*, 2010)

3.4.2 Root

On the 8th and 9th of May, the soil of every pot was sieved through a 0.2 mm mesh to catch and retain roots (Figure 8). Roots were carefully washed with distilled water to remove soil particles. They were sponged gently to clear the water in excess and weighed to determine their saturated mass (SM). Roots samples were divided into three subsamples. The first two weighed 0.2g and were analysed for roots architecture and mycorrhizal colonisation. Both samples were immersed in a 70% ethanol solution and stored in a 4°C refrigerator (Guo *et al*, 2004; Holdaway *et al*, 2011 ; Yahara *et al*, 2019). The remaining part of the roots were dried in a 40°C oven for 72 hours and weighed in order to measure the root dry mass.



Figure 8: Root Harvest

3.4.2.1 Roots Architecture

Prior to scanning, roots samples were carefully spread out in 70% ethanol solution on petri dishes. The roots were digitalized at 400 dpi with a scanner (Epson Perfection V800) to be analysed with EZ-Rhizo (Glasgow Univ., UK), see Figure 9. The software automatically determined the roots length and number of tips. Branching intensity was calculated as the number of tips divided by the total length of the sample (Comas & Eissenstat, 2009).

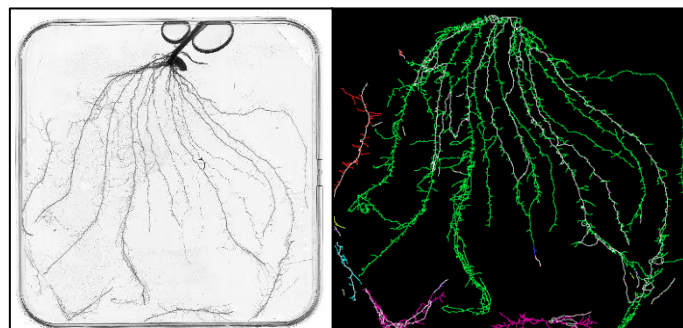


Figure 9: Scanned roots analysed with EZ-Rhizo

3.4.2.2 Roots Mycorrhizal Colonisation

Four pre-tests were run based on the method developed by Vierheilig *et al.*, 1998. The most efficient result was found when the roots were covered with 10% KOH at 85°C for 45 minutes, then with HCl 1% at room temperature for an hour before being stained with ink-vinegar solution at 85°C for another hour (Figure 10 A). Roots laid overnight in this solution made of a litter of household vinegar (7%) mixed with 57mL of Parker black Quink ink (Parker Pen USA Ltd., Janesville, USA). Afterwards, roots were stored in 50% glycerine solution for 7 days letting them decolour.

Thereafter, root samples were cut into pieces of about 1 cm in length and placed in parallel on a glass slide (Figure 10 B). Few droplets of glycerine were added before pressing a cover slide on the roots. Sampled roots were observed under microscope and root length colonization (RLC %) were assessed using systematic gridline-intersect method (Giovenetti & Mosse, 1980).



Figure 10: Assessing roots mycorrhizal colonisation
A: Staining at 85°C B: Microscope observation

3.4.3 Silicon, nutrient and pH Analysis

Dry stems and leaves material were grounded to a fine powder to analyse the total major nutrients (magnesium (Mg), calcium (Ca), sodium (Na), potassium (K), manganese (Mn), iron (Fe) and aluminium (Al)) concentration (expressed as a percentage of dry mass) by inductively coupled plasma spectrometry (ICP-AES) after calcinations at 450°C followed by HF-HClO₄ digestion (Ciesielski *et al.*, 1997). Soil total Si concentration was determined by ICP-AES after calcination at 450°C followed by fusion at 1100°C in a Pt/Rh crucible with 0.2 g of Li-tetraborate and 0.8 g Li-metaborate (Voinovitch *et al.*, 1962).

The bioavailable Si pool concentration was assessed by CaCl₂ extraction (Si_{cc}). Homogeneous 5g-samples of every 42 soils were mixed with 50 mL of CaCl₂ 0.01M (Sauer *et al.*, 2006). The solution was shaken for 16 hours at slow speed to avoid quartz abrasion (McKeague & Cline, 1963). Then the supernatant was filtered with Whatman 620 (Whatman Reeve Angel Ltd., Maidstone, UK) before pH analysis (Figure 11). Si, Fe and Al contents were then quantified using ICP-AES. The amount of Si released in the extract represents the immediately available Si fraction for plant uptake (Berthelsen *et al.*, 2001; Cornelis *et al.*, 2011).



Figure 11: Extraction of bioavailable silicon extracted with CaCl_2

3.4.4 Statistical analyses

Statistical analyses were performed using R (R Development CoreTeam, 2006) for analysis of variance, means, standard errors and repeated measurement data. Statistically significant differences between treatment means were considered at the 5% level ($p > 0.05$). The shapiro wilk test was performed to check the normality of the distribution of continuous variables because it represents the most powerful test especially for variables with small numbers (Razali *et al.*, 2011).

4 RESULTS

The measures of the dissolved Si extracted from the pots substrates with CaCl_2 (Si_{cc}), the Si content in the shoots (Si_{abs}) and the substrate pH are presented as the mean of the 6 replicates of each group (Table 1). As a general point of view, the controlled warm and drought conditions in the second chamber reduced significantly the Si_{abs} (-31%, p-value = 0.044) of the rice shoots. However, the Si_{cc} and the pH show no significant differences between the two climates.

Overall, the controlled inputs of PhSi are significantly correlated with the Si_{cc} (p-value < 0.001) and the Si_{abs} (p-value = 0.013). Indeed, the Si_{cc} tends to increase as the input of PhSi increases (see Figure 12B). However, the differences between the levels of inputs show a significant increase in the Si_{cc} content only between the first and the third level of inputs of the optimal chamber (i.e. groups O1 and O3). No significant differences were found in the warm chamber. Meanwhile, the Si_{abs} shows significant differences between the first two levels of inputs of the warm chamber only (i.e. groups W1 and W2, see Figure 12A). As a matter of fact, the contrastive environmental factors seem to have no impact on the pH.

Table 1: Impact of the environmental factors on silicon in soil and plants and on the pH

Environmental factors			Responses (mean \pm sd)		
Climate	PhSi [mg/kg]	Groups	Si_{cc} [mg/kg]	pH cc	Si_{abs} [%DM]
Optimal	0	O1	5,43 \pm 0,85 a	5,59 \pm 0,51 a	2,54 \pm 0,92 a
	1000	O2	8,83 \pm 2,62 ab	6,14 \pm 0,58 a	3,73 \pm 1,04 a
	2000	O3	9,67 \pm 1,84 b	5,87 \pm 0,48 a	4,43 \pm 2,44 a
Warm	0	W1	6,53 \pm 1,03 ab	5,54 \pm 0,45 a	1,44 \pm 0,62 b
	1000	W2	8,83 \pm 1,79 b	5,83 \pm 0,62 a	3,16 \pm 1,61 a
	2000	W3	10,03 \pm 3,02 b	5,42 \pm 0,46 a	2,81 \pm 1,36 ab

Results are shown as the mean of the 6 replicates for each modality \pm standard deviation. Silicon content in shoot are represented in % of shoot dry mass. Soil pH and Si content were assessed after CaCl_2 extraction. Means followed by different letters in columns are significantly different by T-test with 5% confidence interval ($p \leq .05$).

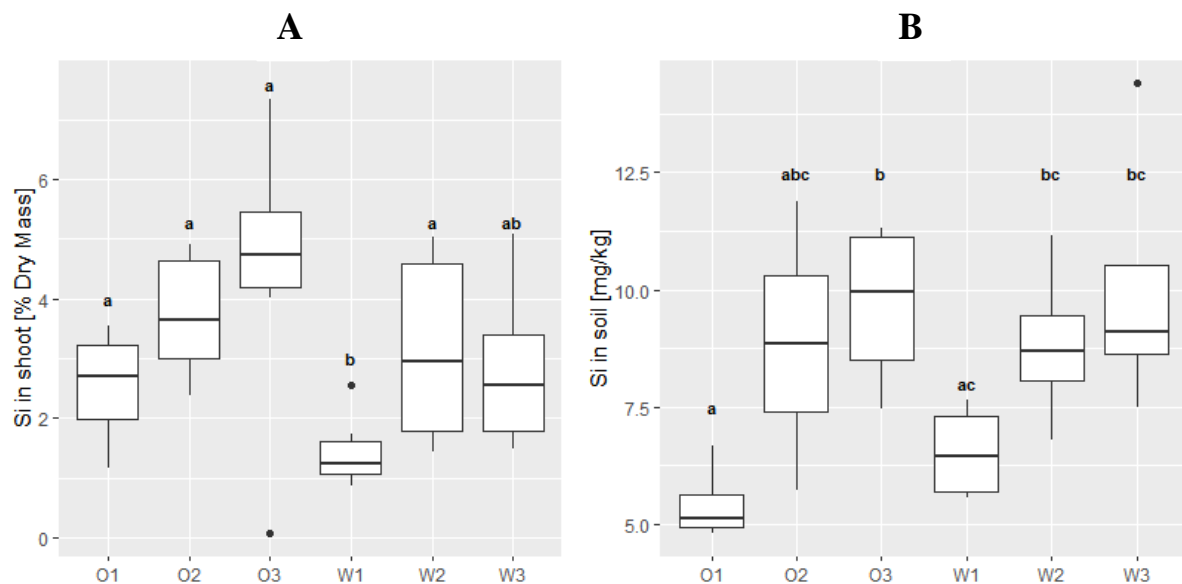


Figure 12: Silicon content assessed with ICP-AES A: Si_{abs} in shoot (borate fusion) B: Si_{cc} in soil (CaCl_2 extraction). Means followed by different letters above the boxes are significantly different by T-test with 5% confidence interval ($p \leq .05$).

There is a correlation between the Si_{cc} and the Si_{abs} (p-value = 0.046) which is illustrated with the figure 13. At similar amount, unstressed plants have absorbed more Si and this value is better suited with the Si content in the pots (see figure 14). This difference is highlighted regarding the coefficient of determination ($R^2_{opt} = 0.516$; $R^2_{warm} = 0.128$).

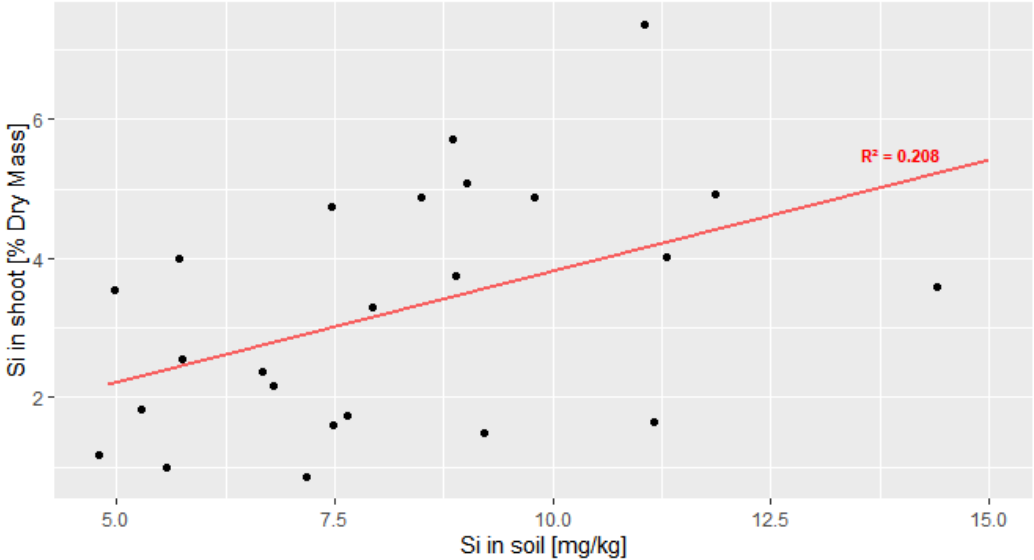


Figure 13: Correlation between Si in soil (CaCl₂ extraction) and Si in shoot (all data presented). Linear regression and associated coefficient of determination are shown in red.

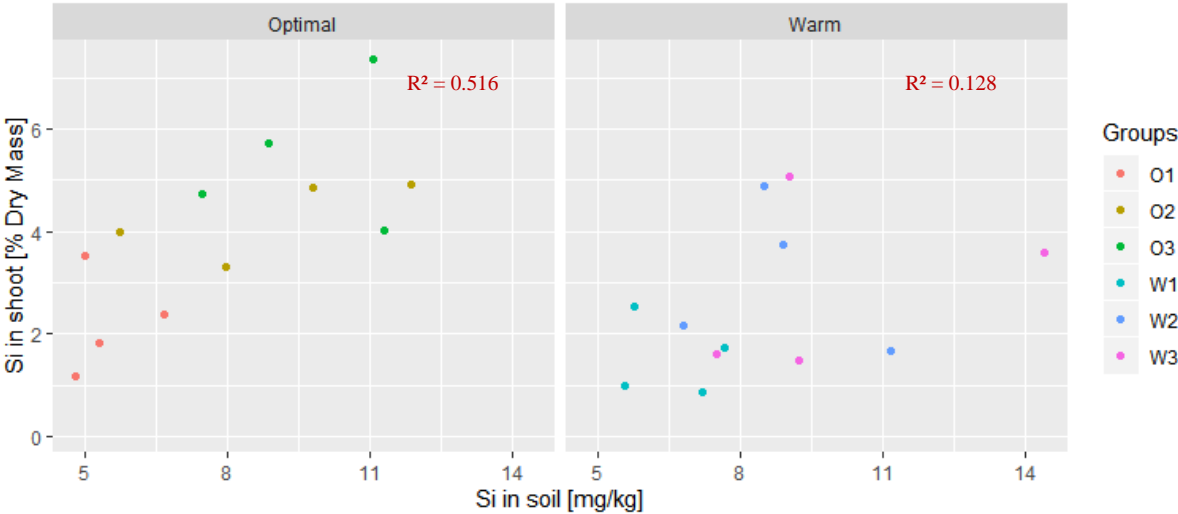


Figure 14: Correlation between silicon in soil (CaCl₂ extraction) and silicon in shoot, all data presented by chambers. Groups are shown in different colours. Coefficient of determination is shown in red for both culture chamber.

The measures of the main aboveground and belowground traits are presented as the mean of the 6 replicates of each plant group (Table 2). The correlation between those traits have been figured in the form of a matrix (Figure 15). Overall, the augmentation in the Si content tends to increase the biomass (Table 1) and significantly increases the plant height in the optimal chamber (Table 3). However, there was no other significant increase in the measured yields traits alongside the increase of PhSi in none of the two chambers. Both the leaf arc and the leaf area tend to increase with PhSi inputs. They also are well correlated with the biomass traits. The specific leaf area (SLA) decreases with the input of PhSi (p-value = 0.031) but not significantly with the Si_{abs} (in both chambers). Regarding to the groups, the relation between Si and SLA is only significant between the W3 plants group and the rest, W2 excepted.

Table 2: Results of the main trait responses to the environmental factors

Treatment	Plant responses (mean ± sd)								
Groups	Roots Mass [g]	Shoot Mass [g]	Leaf Area [cm ²]	SLA [cm ² /g]	Branching Intensity	LDMC	Leaf Arc	Al [mg/kg]	Fe [mg/kg]
O1	0,518 ± 0,26 a	1,18 ± 0,63 a	24,3 ± 13 a	160,5 ± 22,7 a	2,08 ± 0,19 a	0,204 ± 0,013 a	5,0 ± 2,8 a	2,27 ± 1,4 a	0,359 ± 0,18 a
O2	0,645 ± 0,58 a	1,68 ± 2,2 a	28,1 ± 31 a	160,0 ± 25,5 a	2,37 ± 0,28 ab	0,197 ± 0,012 a	4,4 ± 4,2 a	0,344 ± 0,20 a	0,265 ± 0,21 a
O3	0,665 ± 0,31 a	1,76 ± 0,82 a	31,1 ± 8,3 a	142,5 ± 32,0 a	2,57 ± 0,13 b	0,223 ± 0,060 ab	6,5 ± 2,9 a	0,706 ± 0,65 a	0,246 ± 0,09 a
W1	1,19 ± 1,1 a	1,90 ± 1,9 a	25,7 ± 21 a	138,1 ± 16,5 a	2,40 ± 0,25 b	0,330 ± 0,23 ab	3,3 ± 3,6 a	1,63 ± 1,8 a	0,491 ± 0,21 a
W2	0,914 ± 0,73 a	2,55 ± 2,0 a	31,9 ± 19 a	127,9 ± 34,9 ab	2,46 ± 0,24 b	0,238 ± 0,069 ab	4,3 ± 3,1 a	1,62 ± 2,1 a	0,341 ± 0,20 a
W3	1,46 ± 1,2 a	2,63 ± 2,0 a	29,7 ± 20 a	97,99 ± 30,3 b	2,55 ± 0,13 b	0,240 ± 0,018 b	5,2 ± 2,6 a	1,59 ± 1,7 a	0,370 ± 0,21 a

Results are shown as the mean of the 6 replicates for each modality ± standard deviation. Biomass, fresh weight of shoot and roots. Leaf arc measured on the 3rd older leaf. SLA, specific leaf area. LDMC, leaf dry mass content. Means followed by different letters in columns are significantly different by T-test with 5% confidence interval (p ≤ .05).

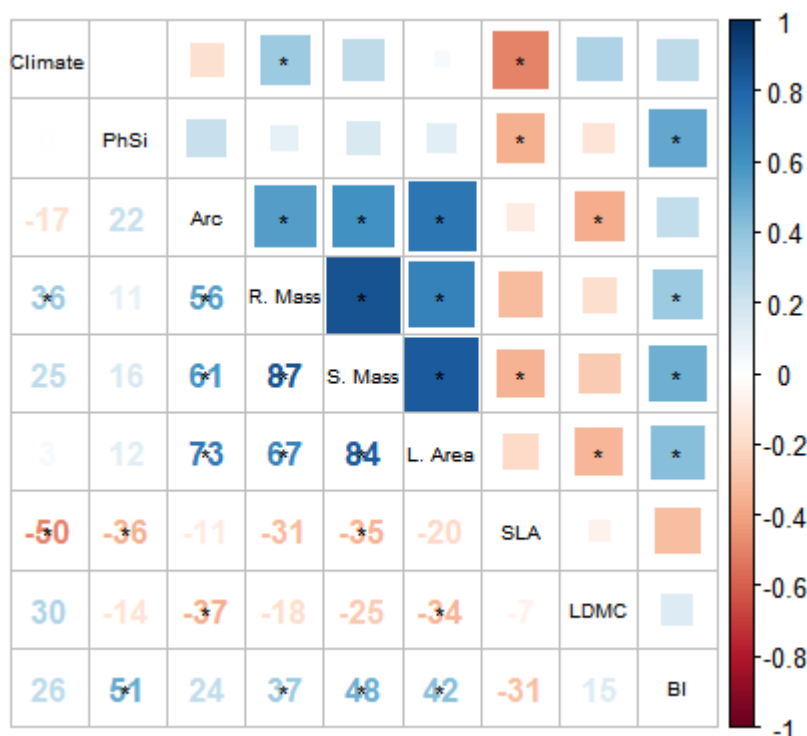


Figure 15: Correlation matrix (All data are presented) was generated on R-studio. Significant relations are shown with "*" (p-value < 0.05). Coefficients of correlation are shown as percent (lower triangle). Climate (chamber) and PhSi (silicon input) represent the qualitative factors of the environments. Arc, leaf arc. R. Mass, root mass. S. Mass, shoot mass. L. Area, leaf Area. SLA, specific leaf area. LDMC, leaf dry matter content. BI, branching intensity.

The climate is also strongly linked with the SLA. The negative correlation means that the SLA is smaller when stressed condition were imposed (-21%, p-value = 0.002). Additionally, the second chamber has a tendency to increase the measured yield traits, with a significant increase in the height (+38%, p-value = 0.010), root mass (+95%, p-value = 0.029) and stem mass (+151%, p-value = 0.011) but the increase in leaves – wet and dry - mass and the overall biomass (p-value = 0.078) are not significant. The trend in the warm chamber has not influence the LDMC. Noticeably, the mass of the leaves is positively linked with the arc (p-value < 0.001) and negatively linked with the SLA (p-value = 0.0131).

No mycorrhizal colonisations were found in any of the roots. However, there is a strong correlation between the branching intensity and the input of PhSi. Indeed, plants supplied with PhSi have more tips on their roots (+11%, p-value = 0.013). This relation is more important in the optimal chamber where the branching intensity of the roots supplied with 2000mg/kg of PhSi is 24% higher (p-value = 0.002) than controlled plants. On the other hand, the increasing trend in the warm chamber shows no significant differences in term of branching intensity between the levels of PhSi inputs. However, the warm chamber shows a negative correlation between the branching intensity and the Si, Ca, Na, and Mg content in leaves. This relation has to be linked with the biomass production as all three variables are related one with another.

Indeed, the calcium and magnesium concentrations are negatively correlated with the height, shoots and roots masses. Concerning the sodium and potassium, this relation is significant only with the shoot mass but there is a trend for all measured element of having a smaller concentration when the rice plants have higher yield traits (result not shown). Unlike Si, there is no real effect of the climate on the minerals shoot concentrations. The initial PhSi concentration in the pots seems to have an impact on Aluminium in the optimal chamber only (Table 3). The plants have absorbed Ca, Mg, Mn and K on similar ratios. The six modalities have poor impact on the nutrients absorbed by the plants.

Table 3: Nutrient absorption by plants in term of environmental factors

Treatment	Plant responses (mean ± sd)								
Groups	Silicon [%DM]	Calcium [%DM]	Aluminium [%DM]	Iron [%DM]	Potassium [%DM]	Magnesium [%DM]	Manganese [%DM]	Sodium [%DM]	
O1	2,54 ± 0,92 a	0,399 ± 0,16 a	1,74E-02 ± 0,016 a	0,0131 ± 0,0085 a	2,72 ± 1,05 a	0,42 ± 0,20 a	0,119 ± 0,041 a	1,72E-01 ± 0,21 a	
O2	3,73 ± 1,0 a	0,378 ± 0,12 a	9,99E-03 ± 0,014 ab	0,0118 ± 0,0076 a	2,93 ± 0,27 a	0,38 ± 0,074 a	0,109 ± 0,028 a	4,74E-02 ± 0,073 a	
O3	4,43 ± 2,4 a	0,233 ± 0,11 a	5,93E-04 ± 0,0015 b	0,0068 ± 0,0034 a	2,64 ± 1,31 a	0,26 ± 0,13 a	0,104 ± 0,054 a	6,01E-02 ± 0,042 a	
W1	1,44 ± 0,62 b	0,525 ± 0,41 a	1,37E-03 ± 0,0017 ab	0,0150 ± 0,013 a	3,46 ± 1,33 a	0,47 ± 0,21 a	8,55E-02 ± 0,028 a	6,83E-02 ± 0,073 a	
W2	3,16 ± 1,6 a	0,275 ± 0,056 a	0,00E+00 ± 0,000	0,0071 ± 0,0038 a	2,52 ± 0,66 a	0,29 ± 0,075 a	7,59E-02 ± 0,023 a	1,71E-02 ± 0,022 a	
W3	2,81 ± 1,4 ab	0,442 ± 0,31 a	2,62E-03 ± 0,0060 ab	0,0155 ± 0,015 a	3,86 ± 2,61 a	0,41 ± 0,32 a	0,110 ± 0,11 a	3,34E-02 ± 0,016 a	

Results are shown as the mean of the 6 replicates for each modality ± standard deviation. All data presented. Nutrient concentration as the percent of dry mass of the shoot. Means followed by different letters in columns are significantly different by T-test with 5% confidence interval ($p \leq .05$).

5 DISCUSSION

5.1 Influence of the Silicon

5.1.1 Direct effect of Silicon

The increase of dissolved Si in the substrate due to the PhSi inputs has increase the intake of Si by the rice plants. Plants grown in optimal conditions have significantly absorbed more silicon than stressed plants despite no real differences in soil extractable (with CaCl₂) Si content. These results are comparable to those obtained by Sistani *et al.* (1997) in a greenhouse experiment on rice supplied with rice hull ash (Table 4). The 1997 experiment grew hundreds of plants for 5 weeks on soils not Si depleted. The time and the number of seedlings per pot might partially explain the differences in nutrient absorption and height, respectively. The mineral absorption are similar to the results of Tavakkoli *et al.* (2011) who grew rice on a highly weathered soil. The fact that the differences of Si content between the groups are very similar between the two experiments (1997/2020) may indicate that this experiment failed to create a Si depleted substrate for the plants. Creating Si free environments represent the main difficulty for assessing the benefits and essentiality of Si (Liang *et al.*, 2015). As expected, rice plants have accumulated more Si than any other nutrient (Ma & Takahashi, 2002). The current study also shows that the increase in Si content “corresponds with the decrease in Al contents” (Sistani *et al.*, 1997). Si has a crucial role in reducing the ecotoxicity of Al in every ecosystem due to the co-precipitation in hydroxyaluminosilicate (Birchall *et al.*, 1989; Beardmore *et al.*, 2016). However, in the case of plants stress alleviation, it is unclear whether the complexation reaction occurs in the growth medium, in the roots or in the shoots (Wang *et al.*, 2004; Guntzer *et al.*, 2011; Cooke & Leishman, 2016). The present study might give an insight that the addition of Si acts on Al toxicity by preventing its translocation in the shoots.

Table 4: Comparison between the current study and results from Sistani *et al.*, 1997

Experiment	Plant responses								
	RHA (T/ha)	Plant Ht [cm]	Shoot Dry Wt [g]	Si [%DM]	Al [mg/kg]	Fe [mg/kg]	K [mg/kg]	Mn [mg/kg]	
Present Study	0	21,6 a	0,244 a	2,54 a	1,74 a	1,3 a	272,2 a	11,9 a	
	3,45	23,9 ab	0,317 a	3,73 a	1,00 ab	1,2 a	293,5 a	10,9 a	
	6,9	27,8 b	0,365 a	4,43 a	0,06 b	0,68 a	263,7 a	10,4 a	
Sistani <i>et al.</i> , 1997	0	44,5 x	0,166 y	1,92 z	0,51 y	0,39 x	27,5 z	4,10 x	
	5	48,5 y	0,187 z	3,08 x	0,45 y	0,43 x	28,9 z	3,27 y	
	10	52,8 y	0,188 z	3,86 y	0,41 y	0,39 x	33,6 y	2,88 z	

Results are shown as the mean of each modality. Present study shows results of the optimal chamber. Sistani *et al.* results are presented as the average of two rice cultivars, three soils, and three replicates grown for 5 weeks. RHA, Rice Hull ash. Ht, height. Wt, Weight. %DM, percentage of shoot dry mass. Means followed by the same letters in each column are not significantly different at the 5% confidence level, means of the two studies have not been compare one with the other.

Unlike the experiment of 1997, this experiment did not show significant differences concerning the K and Mg content between the groups. However, in both experiments, the addition of rice hull ash results in an increase in the plant height, indicating an impact of Si on the plant growth.

Indeed, the root and shoot biomasses likely increase with the level of PhSi but the low variability inter-group and the large variability intra-group avoid any conclusion on a direct relation. This link has the indirect effect of increasing the leaf arc with the PhSi, but the impact of Si on the erectness of the leaves is insignificant. The arc of the leaves is positively correlated with their weight and negatively correlated with the dry matter content, designating the water content as the main factor influencing the erectness

of the leaves (p-value = 0.003), result not show. On the other hand, Si in the shoot is not correlated with the LDMC.

5.1.2 Influence of the pH on nutrient dissolution

The pH of the substrate greatly influences the dissolution and the mobility of the nutrients. During the experiment, the pH in the pots varies between 5 and 7 which is in the good range for essential nutrient availability and in the range of maximum Si absorption by rice plants on weathered soils (Tavakkoli *et al.*, 2011). Data compute from 14 field experiments show that Si maximum extractable rate with CaCl_2 are around pH 6-7 (de Tombeur *et al.*, 2020a). The present experiment stands with these observations as Si_{cc} increases along this pH interval (p-value = 0.030), see figure 16 A. Contrastively, the dissolution of Al and Fe ions is high at acidic pH and decreases with the neutralisation of soil solution (Figure 16 B - C).

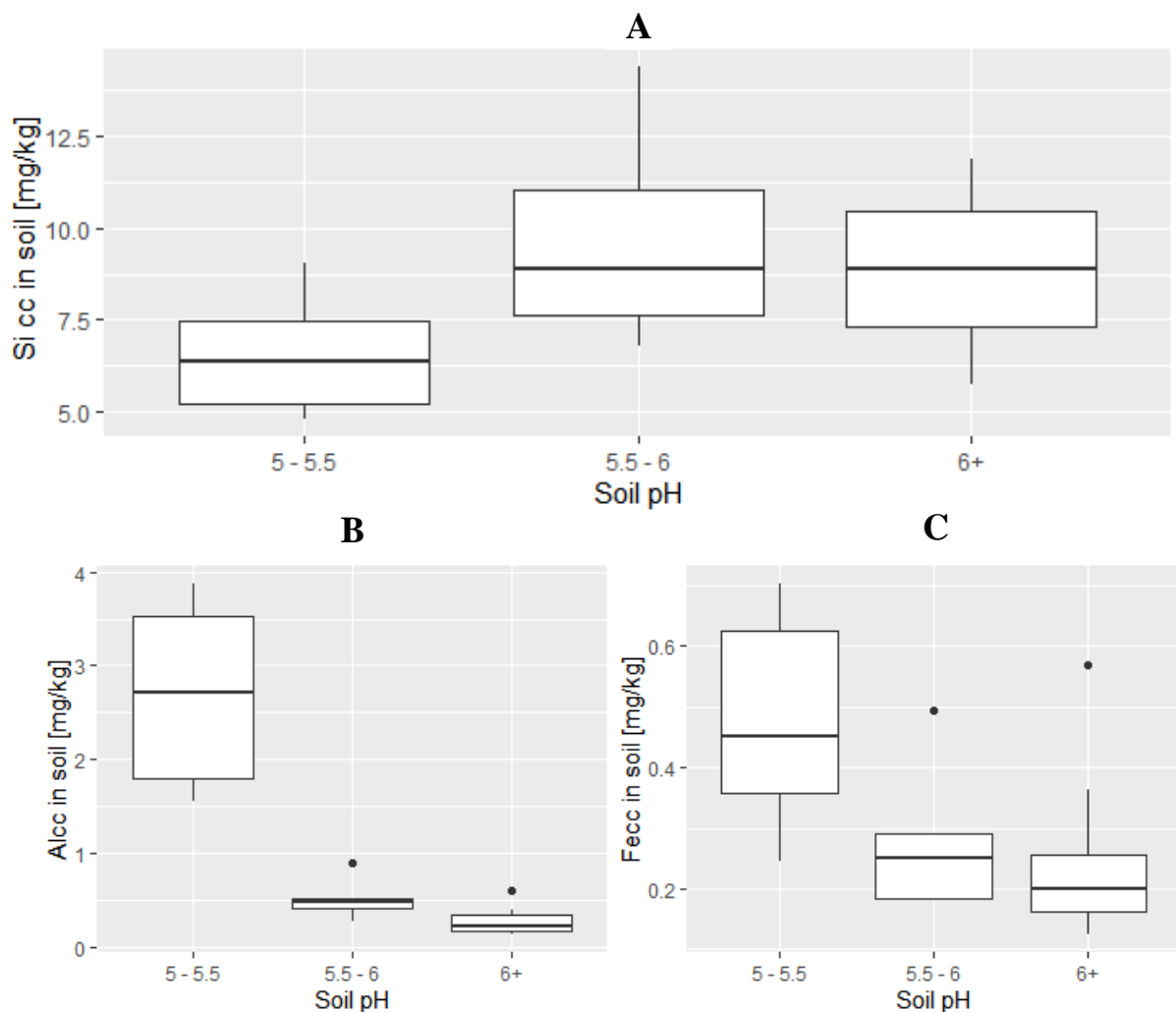


Figure 16: Influence of the pH on the dissolution of A: Silicon, B: Aluminium, C: Iron. All data presented. Mean and standard deviation represent the concentration in soil extracted with CaCl_2 .

5.2 Interaction between Silicon and Climate

5.2.1 Influence of the environmental factors

The elevation of temperature and the withholding of water did not affect the biomass production of the rice plants. This result, which might seem unforeseen, is actually not surprising in the light of the literature. Indeed, rice plants exposed to a higher maximum temperature often show no negative growth signs (Peng *et al.*, 2004; Krishnan *et al.*, 2007; see also Johnson & Hartley, 2017 for other grass species and Zhao *et al.*, 2017 for a review on the main crop species) and even sometimes an increase in the biomass production (Ziska *et al.*, 1997; Cheng *et al.*, 2009; Welch, 2010). However, the tendency to increase biomass under warmer conditions does not mean the plant has not found itself in a stressful condition or that its yield has not been impacted (Omasa *et al.*, 1996; Cheng *et al.*, 2009). On the contrary, the stress induced by climatic conditions pushes the plant to use a strategy of faster growth and acceleration of its metabolism (Oh-e *et al.*, 2007). This survival strategy is, however, dependent on the number and quality of its grains, which are essential indicators to qualify its yield (Li *et al.*, 2014). The results of this experiment show that the plants placed in the stress chamber certainly used this survival strategy because they grew significantly faster and higher but without really increasing their biomass. This growth took place at the expense of the concentration of essential minerals which could have resulted in a decrease in spikelet fertility and quality.

Hence, the lack of water did not result in the reduction of the leaf size nor in the shortening of the stem and the roots as it is expected with ordinary drought stress (Farooq *et al.*, 2009) and with the combination of stresses. The concomitant elevation of temperature and withholding of water is, most of the time, causing more severe damages than both stresses alone (Suzuki *et al.*, 2014). Indeed, the water stress induces the closure of the stomata which reduces the photosynthesis and increases leaf temperature, both consequences are exacerbated by the elevation of temperature (Mittler & Blumwald, 2010). Moreover, warmer conditions were shown to inhibit the production of antioxidants responsible for drought resistance. These results indicate that the mode of actions that alleviate these concurrent stresses are the maintenance of photosynthetic activity and the production of osmoprotectants (Suzuki *et al.*, 2014).

5.2.2 Role of the Silicon

On the other hand, Si is known to enhance nutrient absorption, stomatal conductance – and subsequently photosynthesis –, water balance, water potential, roots proliferation, accumulation of osmolytes and osmoprotectant synthesis and to reduce transpiration losses (Farooq *et al.*, 2009; Guntzer *et al.*, 2011; Rodrigues & Datnoff, 2015; Cooke & Leishman, 2016; Debona *et al.*, 2017; Etesami & Jeong, 2018).

Those acclimations might have helped the plant of this experiment to reverse the adverse effects of the combined stresses. However, the analysis of the results did not show any significant differences between the levels of Si inputs in the warm chamber. Two hypothesis can therefore be drawn; (1) the stress imposed to the rice plants was not severe enough to demonstrate any adverse effect or (2) the plants which did not receive any PhSi input (i.e. W1) found enough Si in the substrate to buffer the potential positive effects of Si. The controlled plants have, indeed, concentrated Si at a rate of about 2% of their dry weight. This amount classifies them largely as hyperaccumulators but more importantly, some studies have revealed significant effects at similar rates such as the increase of water and nutrient uptake which maintains the biomass production, allowing leaf expansion and high photosynthetic rates (e.g. Ming *et al.*, 2012; Tavakkoli *et al.*, 2011; Fleck *et al.*, 2015).

5.2.3 Belowground traits

5.2.3.1 Branching intensity

One element of the answer is in the belowground traits. The root proliferation, the number of secondary roots and therefore, the branching intensity are the main characteristics increasing the water and nutrient uptake. Branching intensity is an important adapting trait of plant to their contrastive environment (Holdaway *et al.*, 2011). The Si supplies increased the number of tips per roots in the optimal chamber (Figure 17) which may have induced higher biomass (shoot and roots) production (p-value = 0.005) and wider leaf surface (p-value = 0.001). Secondary roots may have contributed to increase the concentration of Si and other nutrients in the shoots (Ma *et al.*, 2001). However, none of these traits show significant increases between the levels of PhSi inputs.

Between the groups of plants with no PhSi inputs, the one in the warm chamber have a higher branching intensity, indicating that the stress led the plants to increase the number of secondary roots. However this increase is not significant for the plants supplied with Si between the chambers nor within the different groups inside the warm chamber. Unfortunately, at this stage, it is impossible to draw more definitive conclusions from this study.

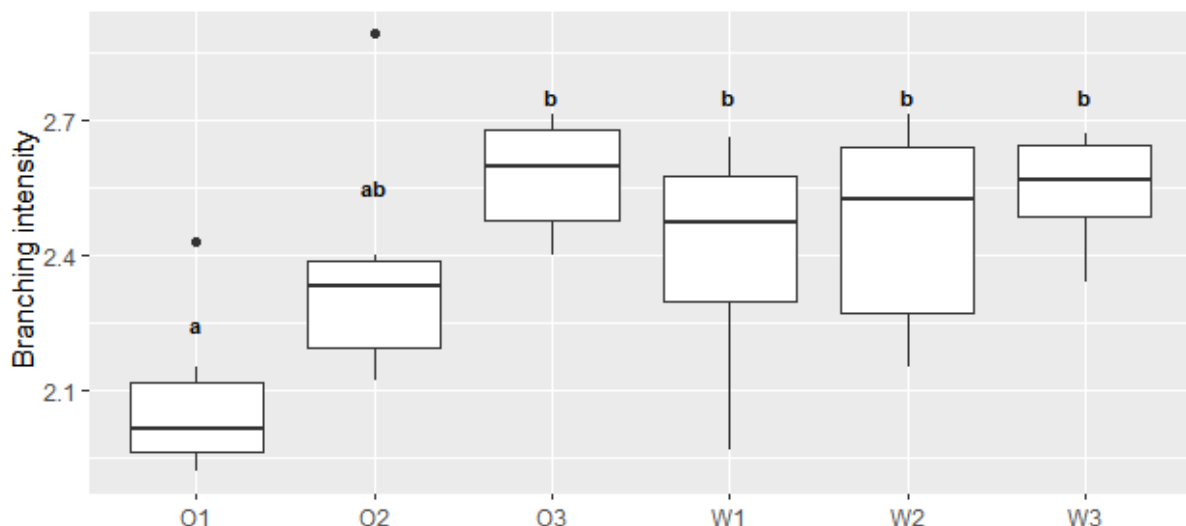


Figure 17: Results of the branching intensity, all data presented as the mean and standard deviation of each modality. Means followed by different letters above the boxes are significantly different by T-test with 5% confidence interval ($p \leq .05$).

5.2.3.2 Mycorrhizal Colonisation

The microscopic observations revealed that the roots have developed normally (Morita & Nemoto, 1995) and the stain has succeed (see Figure 18) but no mycorrhizal apparatus have been found in any of the roots despite the propagules inoculation. The nutrient concentrations in the substrate and especially the phosphorus (P) are the main factors hindering the roots colonisation (Graham *et al.*, 1982; Vierheilg, 2004). The P concentration added in the pots with the nutrient solution was first believed to be far from any threshold; a total of 260 mg of P has been supplied through the nutrient solution during 4 weeks, corresponding to a maximal concentration of 34.6 mg/kg in every pots which is in the range of normal fertilization (Kalala *et al.*, 2016) and below P threshold (Menge *et al.*, 1978; Graham *et al.*, 1982; Yost & Fox, 1982). However, the bioavailable P was certainly too high from optimal mycorrhizal growth conditions due to the high solubility of the phosphate inside the nutrient solution (Maiti *et al.*, 2011; Maiti & Barnwal, 2012; Verbruggen *et al.*, 2012). Nevertheless, the fact that absolutely no fungi

structure was found in the roots makes it more likely to be an incompatibility between species, a problem during the transport or during the inoculation than a hostile environment to AMFs.



Figure 18: Roots mycorrhizal colonisation observation under microscope

5.2.4 Aboveground traits

5.2.4.1 Specific Leaf Area (SLA)

Drought and elevation of temperatures reduce the SLA (Zhou *et al.*, 2019). Water scarcity is the main cause of this reduction because of the decrease in the nutrient uptake (Holdaway *et al.*, 2011) which prevents the leaf growth and therefore reduces the leaf surface (Wopereis *et al.*, 1996). Si supplies may have reversed the adverse effects of the combined stresses on the leaf dry weight and the leaf surface (see belowground traits; Parent *et al.*, 2010) but Si augments the decrease of the SLA. These results are consistent with the one reported by Gong *et al.* (2003). Indeed, the leaf dry weight increases more sharply than the leaf surface. In other words, Si increases the thickness of the leaves and therefore reduces the SLA (Figure 19). Thicker leaves improve the regulation of water within the plant by reducing the transpiration rates and improving photosynthetic rates (Niinemets, 2001). This change in the physiology of the rice plant might be an important component of the stress resistance induced by Si.

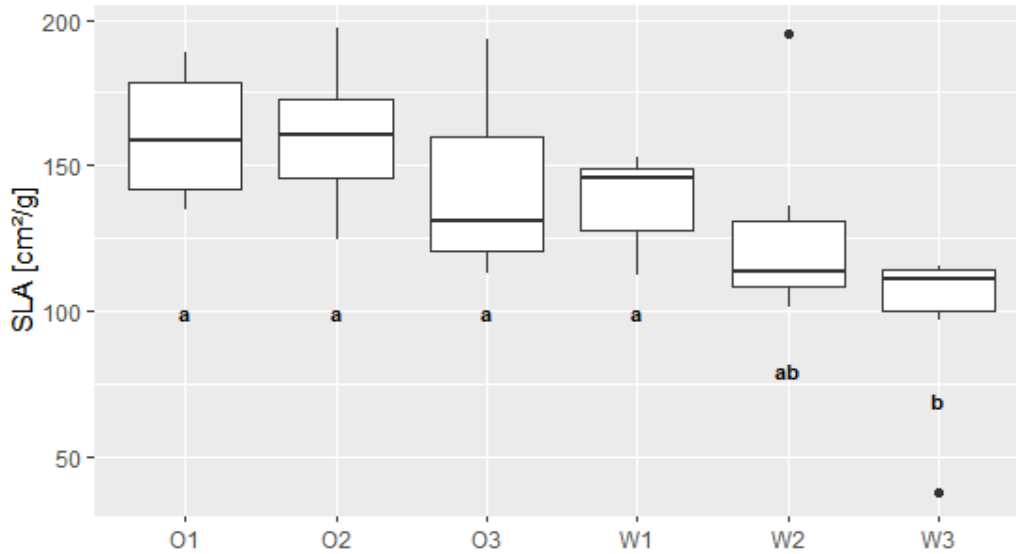


Figure 19: Results of the specific leaf area. All data were used and they are presented as the mean and standard deviation of each modality. Means followed by different letters under the boxes are significantly different by T-test with 5% confidence interval ($p \leq .05$).

5.3 Variability

The results of this experiment show clear tendency of the hypothetical impacts of the climate and the concentration of PhSi in the pots substrate on the rice plants (*Oryza sativa* subsp Koshihara). The aboveground and belowground traits based approach helped the understanding of the mechanisms of stress alleviation induced by Si supplies. However, most of the groups means suffer from huge intrinsic variability which is hindering the drawing of real relations between the controlled climatic factors and the measured traits. Indeed, only the pH, LDMC and the branching intensity have a standard deviation sometimes inferior at 10% of the group means. Some hypothesis have been assumed to be the cause of the variability of the plants responses inside the groups of common modalities. The first one is the probable heterogeneity of the environmental conditions inside both culture chambers. Indeed, the pots have been placed in three rows of seven (see Figure 20) and the third row (i.e. the farthest of the doors) has shown different signs of drier conditions in both chambers. The first sign was the colour of the surface of the substrate. From the first day of the experiment, the Hydro A+B nutrient solution was applied in the same concentration, among the same quantity of irrigation water and at the same time for every single pot of the experiment. This nutrient solution has a red coloration which coloured the surface of the third-row-pots only, reflecting higher evaporation rate. This light sign has been supported in the beginning of the third week with the apparition of green moss on the first and second row only (see Figure 20).



Figure 20: Heterogeneity of green moss development in culture chambers

The assumption was that the lower water content of the third row did not allow the green moss to grow. Meanwhile, the plants of this row began to show signs of drier conditions in both chambers. Indeed, plants were growing more slowly with less erected leaves, sometimes yellowish. The cause of this heterogeneity may have been the size of the pots which was obstructing the convection of the air inside the chambers. Big sized pots were chosen to be sure to not hinder the growth and the spreading of the roots but they rendered the daily switching (commutation) impossible. It was thus decided to take a replicate of each modality out of the chambers to be able to commute them and avoid the chamber heterogeneity more easily. The second hypothesis of the cause of the variability of the responses of the plants inside the groups of equal environmental modalities is the number of plants left to grow during the experiment. Indeed, a unique plant per pot is more sensitive and less resilient and thus can increase contrastive responses especially when the conditions are not perfectly identical.

Nevertheless, the significant relations between the PhSi inputs and the Si_{abs} coupled with the results of the height, the branching intensity and the SLA indicate that the plants in the warm chamber have experienced stressful conditions which was partially reversed by the rice hull ash supplies.

6 PERSPECTIVES

It is important to note that this experiment was carried out during the coronavirus crisis at the beginning of the year 2020. This situation constrained to change the operator in the heart of the process which results in an obvious bias. In addition, a large number of analyses could not be carried out, for instance the mechanical resistance tests of the leaves, the analysis of nutrients in the roots or the ^{13}C ratio. Each of these traits could have allowed a more detailed analysis of the strategy adopted by the plants subjected to the stress combination as well as the influence of silicon on it. Still, several perspectives are to be considered if this subject is to be deepened.

As a first step, some improvements of the experimental protocol must be considered in order to reduce the biases inherent in this study. The first thing would be to make a better choice on the substrate to use by doing analyses on different options in order to choose the substrate that would offer the best anchorage for the plants and a better ability to isolate the effect of the different treatments. Then, an obvious mistake was not to cover the pots, at the bottom with geotextile to prevent the leakage of the elements of the substrate and at the top of the pots to prevent the development of green moss. With regard to the pots, it is evident, given the situation, that a smaller size would have permitted a quicker reaction to the heterogeneity of the culture chamber. This choice was made knowingly to allow perfect freedom of root development. Therefore, it is recommended to anticipate any heterogeneity by preparing a regular pot switching solution because even the best tools have their flaws. Regarding the chambers, it would be wise to know the light intensity since that was certainly lacking during this experience. Regarding the plants, the choice was the right one, in particular for a master thesis since rice allows short-term experiences. It is a resilient plant and one of the best documented, in particular on subjects related to the silicon. However, the specific characteristics of each variety should be known as it can vary within the "*Oryza sativa*" specie. These characteristics will ensure knowledge of the optimal values of controlled plant growth. About the analyses, quantifying available phosphorus in the substrate and in the roots is imperative for future research involving mycorrhizal fungi. More anecdotally, analysing bioavailable Si using water as an extractant seems to show better results than with CaCl_2 (Tavakkoli *et al.*, 2011). Eventually, during ordinary sanitary conditions, it would have been interesting to repeat several water stresses during the growth period because evidence shows that this type of stress is much more complicated to manage for the plants (Vandegeer *et al.*, 2020; Duan *et al.*, 2020)

On another note, the study of the interaction between plant, AMF and silicon needs to be deepened. If Si has, as it is believed, a real impact on the ability of plants to resist to the increased frequency and intensity of future climatic fluctuations, it is surprising that so few studies have looked at its influence on AMFs. Indeed, when exposed to sufficient concentrations of nutrients, plants reinforce the rigidity of their walls to prevent parasitism of once symbiotes fungi (Graham *et al.*, 1982; Vierheilig, 2004). Silicon, independently from other nutrients, has been shown to strengthen the impermeability of root cells in a similar way, preventing parasitic fungi from entering their cells (Bélanger *et al.*, 2003; Duan *et al.*, 2020). Further studies are needed to investigate whether this supposedly blind deposition might negatively influence the colonization of the roots by their symbionts.

7 CONCLUSION

The present study has shown that the return of silicon (Si) via the dissolution of phytoliths in Si-depleted soils enriches the pool directly available for plants, which subsequently increases the concentration of this element in their aerial tissues. This could allow plants to better withstand climatic hazards and in particular the combination of stresses caused by the increase in temperature and the reduction in water resources. This stress combination, which is the most damaging on the globe, is expected to increase in terms of intensity and frequency as a result of current climate change (Suzuki *et al.*, 2014). Si could therefore mitigate the harmful effects by (1) increasing the root biomass and in particular the number of secondary roots and (2) increasing the thickness of the leaves. These two modes of action could help maintain the plant's water potential (by increasing intake and reducing evapotranspiration losses) and maintain the amount of nutrients absorbed. This has the consequence of maintaining or increasing the production of above-ground biomass and the photosynthetic ratio.

More studies are needed in order to conclude that silicon has a direct effect. However, the present experiment gives an insight on the importance of the silicon cycle in the capacity of Si to support ecosystems to avoid climatic stresses. This ability could also help anthropised ecosystems to maintain an acceptable level of production even during the harshest periods of the year, especially crop cultivation. Other studies have shown that conventional agriculture decreases the amount of bioavailable silicon at rates similar to the Si exports to the oceans (Berner & Berner, 2012; Carey & Fulweiler, 2016). Returning Si in the form of hull ash is a great way to maintain the bio-geo-chemical cycling and replenish the DSi pool of agricultural soil. The low cost of hull ash and its wide range of action is a sustainable and affordable way for farmers to increase the resilience of their cultures to environment stressors

The return of silicon through plant litter - i.e. biological Si feedback loop - could register as sustainable land management practices at a time when there is a need for solutions to slow down desertification in the drylands. Indeed, we will end this year the “United Nations decade for deserts and the fight against desertification” but attention must be kept on this problematic because the protection of the soil in the drylands is a major global issue.

8 ANNEX

8.1 Annex 1: Location and soil characteristics of the loamy soil sampling

Map and soil characteristics generated with Wallonmap (<https://geoportail.wallonie.be/walonmap>)



Position physiographique : plateaux et pentes

Matériau textural : **A** sols limoneux

Drainage naturel : **b** favorable (sols non gleyifiés)

Développement de profil (horizon diagnostique) : **a(b)** horizon B textural tacheté **0** horizon A épais: plus de 40 cm d'épaisseur (variante)

8.2 Annex 2: Water Regime

$$ET_o \times K_c = ET_{\text{crop}}$$

$$5.7 \times 1.1 = 6.27 \text{ mm/day}$$

$$[\text{mm} = \text{dm}^3/\text{m}^2] \text{ Surface des pots} = 0.18^2 \text{ m}^2$$

$$6.27 * 0.0324 = 0.20 \text{ L/Jour (1)}$$

$$5.72 * 0.0324 = 0.19 \text{ L/Jour (2)}$$

= 200 mL même chose que Redman et al., 2011

with

ET crop = crop evapotranspiration or crop water need (mm/day)

Kc = crop factor = 1.1 (FAO, 1992)

ETo = reference evapotranspiration (mm/day)

$$ET_o = p (0.46 T_{\text{mean}} + 8)$$

With $p = 0.27$ and $T_{\text{mean}} = 28.5$ (1) et 24.5 (2)

Source: crop water requirement FAO 1992

8.3 Annex 3: Computer code for leaf surface analysis

```
cd(Dossier);

DirRep = dir('*.png');

% Résolution = 72 pixel/cm (via imagej)
SPixel = (1*1)/(72*72);
S = zeros(1,40);

for j = 1 :length(DirRep)

% Import Image j
% -----
    Image = imread(DirRep(j,1).name);
    R = Image (:,:,1);
    Feuille_Totale = (R<0.1);

    A.Surf_Feuille_Totale (j,1) = SPixel*sum(sum(Feuille_Totale));
    S(1,j) = A.Surf_Feuille_Totale (j,1);
end

surf = 'leafarea.xlsx';
xlswrite(surf,S);
```

9 BIBLIOGRAPHY

1. Alexandre, A., Meunier, J. D., Colin, F. & Koud, J. M. Plant impact on the biogeochemical cycle of silicon and related weathering processes. *Geochimica et Cosmochimica Acta* vol. 61 677–682 (1997).
2. Bardgett, R. D., Mommer, L. & De Vries, F. T. Going underground: Root traits as drivers of ecosystem processes. *Trends Ecol. Evol.* **29**, 692–699 (2014).
3. Beardmore, J., Lopez, X., Mujika, J. I. & Exley, C. What is the mechanism of formation of hydroxyaluminosilicates? *Sci. Rep.* **6**, 1–8 (2016).
4. Bélanger, R. R., Benhamou, N. & Menzies, J. G. Cytological evidence of an active role of silicon in wheat resistance to powdery mildew (*Blumeria graminis* f. sp. *tritici*). *Phytopathology* **93**, 402–412 (2003).
5. Berdugo, M. *et al.* Global ecosystem thresholds driven by aridity. *Science (80-.)*. **367**, 787–790 (2020).
6. Berner, E. & Berner, R. Global environment: water, air, and geochemical cycles. (2012).
7. Berthelsen, S., Noble, A. D. & Garside, A. L. Chapter 15 Silicon research down under: Past, present, and future. *Stud. Plant Sci.* **8**, 241–255 (2001).
8. Birchall, J. D., Exley, C., Chappell, J. S. & Phillips, M. J. Acute toxicity of aluminium to fish eliminated in silicon-rich acid waters. *Nature* **338**, 146–148 (1989).
9. Blecker, S. W., McCulley, R. L., Chadwick, O. A. & Kelly, E. F. Biologic cycling of silica across a grassland bioclimosequence. *Global Biogeochem. Cycles* **20**, n/a-n/a (2006).
10. Carey, J. C. & Fulweiler, R. W. Human appropriation of biogenic silicon – the increasing role of agriculture. *Funct. Ecol.* **30**, 1331–1339 (2016).
11. Carpenter, S., Walker, B., Anderies, J. M. & Abel, N. From Metaphor to Measurement: Resilience of What to What? in *Ecosystems* vol. 4 765–781 (2001).
12. Cheng, W., Sakai, H., Yagi, K. & Hasegawa, T. Interactions of elevated [CO₂] and night temperature on rice growth and yield. *Agric. For. Meteorol.* **149**, 51–58 (2009).
13. Cherlet, M. *et al.* *World Atlas of Desertification: Rethinking land degradation and sustainable land management.* (2018). doi:<http://dx.doi.org/10.2136/sssaj1949.036159950013000C0010x>.
14. Chiba, Y., Mitani, N., Yamaji, N. & Ma, J. F. HvLsi1 is a silicon influx transporter in barley. *Plant J.* **57**, 810–818 (2009).

15. Ciesielski, H. & Sterckeman, T. A comparison between three methods for the determination of cation exchange capacity and exchangeable cations in soils. *Agronomie* **17**, 9–16 (1997).
16. Clark, R. B. & Zeto, S. K. Mineral acquisition by mycorrhizal maize grown on acid and alkaline soil. *Soil Biol. Biochem.* **28**, 1495–1503 (1996).
17. Comas, L. H. & Eissenstat, D. M. Patterns in root trait variation among 25 co-existing North American forest species. *New Phytol.* **182**, 919–928 (2009).
18. Cooke, J. & Leishman, M. R. Consistent alleviation of abiotic stress with silicon addition: a meta-analysis. *Funct. Ecol.* **30**, 1340–1357 (2016).
19. Cornelis, J. T. & Delvaux, B. Soil processes drive the biological silicon feedback loop. *Funct. Ecol.* **30**, 1298–1310 (2016).
20. Cornelis, J. T., Titeux, H., Ranger, J. & Delvaux, B. Identification and distribution of the readily soluble silicon pool in a temperate forest soil below three distinct tree species. *Plant Soil* **342**, 369–378 (2011).
21. Coskun, D., Britto, D. T., Huynh, W. Q. & Kronzucker, H. J. The Role of Silicon in Higher Plants under Salinity and Drought Stress. *Front. Plant Sci.* **7**, 1–7 (2016).
22. Coskun, D. *et al.* The controversies of silicon's role in plant biology. *New Phytologist* vol. 221 67–85 (2019).
23. Datnoff, L. E., Deren, C. W. & Snyder, G. H. Silicon fertilization for disease management of rice in Florida. *Crop Prot.* **16**, 525–531 (1997).
- 24.a de Tombeur, F., Turner, B. L., Laliberté, E., Lambers, H. & Cornelis, J. T. Silicon Dynamics During 2 Million Years of Soil Development in a Coastal Dune Chronosequence Under a Mediterranean Climate. *Ecosystems* (2020) doi:10.1007/s10021-020-00493-9.
- 24 b de Tombeur, F., Turner, B.L., Laliberté, E., Lambers, H., Mahy, G., Faucon, M.-P., Zemunik, G., Cornélias, J-T., (2020). Plants sustain the terrestrial silicon cycle during ecosystem retrogression. *Science*, in press.
25. Debona, D., Rodrigues, F. A. & Datnoff, L. E. Silicon's Role in Abiotic and Biotic Plant Stresses. *Annu. Rev. Phytopathol.* **55**, 85–107 (2017).
26. Degenkolbe, T. *et al.* Expression profiling of rice cultivars differing in their tolerance to long-term drought stress. *Plant Mol. Biol.* **69**, 133–153 (2009).
27. Deshmukh, R. K. *et al.* Identification and functional characterization of silicon transporters in soybean using comparative genomics of major intrinsic proteins in Arabidopsis and rice. *Plant Mol. Biol.* **83**, 303–315 (2013).

28. Detmann, K. C., Araújo, W. L., Martins, S. C. V., Fernie, A. R. & DaMatta, F. M. Metabolic alterations triggered by silicon nutrition: Is there a signaling role for silicon? *Plant Signal. Behav.* **8**, 71–74 (2013).
29. Dipankar Maiti & Barnwal, M. K. Optimization of phosphorus level for effective arbuscular-mycorrhizal activity in rainfed upland rice based cropping system. *Indian Phytopathol.* **65**, 334–339 (2012).
30. D’Odorico, P., Bhattachan, A., Davis, K. F., Ravi, S. & Runyan, C. W. Global desertification: Drivers and feedbacks. *Adv. Water Resour.* **51**, 326–344 (2013).
31. Duan, H., Tong, H., Zhu, A., Zhang, H. & Liu, L. Effects of heat, drought and their combined effects on morphological structure and physicochemical properties of rice (*Oryza sativa* L.) starch. *J. Cereal Sci.* **95**, 103059 (2020).
32. Epstein, E. Silicon: its manifold roles in plants. *Ann. Appl. Biol.* **155**, 155–160 (2009).
33. Epstein, E. The anomaly of silicon in plant biology. *Proceedings of the National Academy of Sciences of the United States of America* vol. 91 11–17 (1994).
34. Epstein, E. Silicon. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **50**, 641–64 (1999).
35. Etesami, H. & Jeong, B. R. Silicon (Si): Review and future prospects on the action mechanisms in alleviating biotic and abiotic stresses in plants. *Ecotoxicol. Environ. Saf.* **147**, 881–896 (2018).
36. Exley, C. Silicon in life: A bioinorganic solution to bioorganic essentiality. in *Journal of Inorganic Biochemistry* vol. 69 139–144 (Elsevier, 1998).
37. Exley, C. & Guerriero, G. A reappraisal of biological silicification in plants? *New Phytologist* vol. 223 511–513 (2019).
38. FAO. The future of food and agriculture - Alternative pathways to 2050. Summary version. *Summ. Version 60* (2018).
39. FAO. FAOSTAT. <http://www.fao.org/faostat/en/#data/QV>.
40. FAO. *Trees, forests and land use in drylands: the first global assessment*. FAO Forestry Paper www.fao.org/ (2019).
41. Fao. Crop water requirements. (1992).
42. Farooq, M. *et al.* Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev* **29**, 185–212 (2009).
43. Fauteux, F., Rémus-Borel, W., Menzies, J. G. & Bélanger, R. R. Silicon and plant disease resistance against pathogenic fungi. *FEMS Microbiology Letters* vol. 249 1–6 (2005).

44. Feng, S. & Fu, Q. Expansion of global drylands under a warming climate. *Atmos. Chem. Phys. Discuss.* **13**, 14637–14665 (2013).
45. Fleck, A. T. *et al.* Silicon promotes exodermal casparian band formation in Si-accumulating and Si-excluding species by forming phenol complexes. *PLoS One* **10**, 1–18 (2015).
46. Frew, A., Powell, J. R., Allsopp, P. G., Sallam, N. & Johnson, S. N. Arbuscular mycorrhizal fungi promote silicon accumulation in plant roots, reducing the impacts of root herbivory. *Plant Soil* **419**, 423–433 (2017).
47. Gang, G. Z., Xia, L. H., Rong, W. Y., Min, W. S. & Dong, C. G. Suitability of lucerne cultivars, with respect to root development, to semi-arid conditions in west China. *New Zeal. J. Agric. Res.* **47**, 51–59 (2004).
48. Garg, N. & Singh, S. Mycorrhizal inoculations and silicon fortifications improve rhizobial symbiosis, antioxidant defense, trehalose turnover in pigeon pea genotypes under cadmium and zinc stress. *Plant Growth Regul.* **86**, 105–119 (2018).
49. Gargallo-Garriga, A. *et al.* Opposite metabolic responses of shoots and roots to drought. *Sci. Rep.* **4**, 1–7 (2014).
50. Ghareeb, H. *et al.* Transcriptome of silicon-induced resistance against *Ralstonia solanacearum* in the silicon non-accumulator tomato implicates priming effect. *Physiol. Mol. Plant Pathol.* **75**, 83–89 (2011).
51. Gieseking, J. E. The Clay Minerals in Soils. *Adv. Agron.* **91**, 159–200 (1949).
52. GIOVANNETTI, M. & MOSSE, B. AN EVALUATION OF TECHNIQUES FOR MEASURING VESICULAR ARBUSCULAR MYCORRHIZAL INFECTION IN ROOTS. *New Phytol.* **84**, 489–500 (1980).
53. Gong, H. J., Chen, K. M., Chen, G. C., Wang, S. M. & Zhang, C. L. Effects of silicon on growth of wheat under drought. *J. Plant Nutr.* **26**, 1055–1063 (2003).
54. GRAHAM, J. H., LEONARD, R. T. & MENGE, J. A. INTERACTION OF LIGHT INTENSITY AND SOIL TEMPERATURE WITH PHOSPHORUS INHIBITION OF VESICULAR-ARBUSCULAR MYCORRHIZA FORMATION. *New Phytol.* **91**, 683–690 (1982).
55. Grainger, A. *The threatening desert: Controlling desertification. The Threatening Desert: Controlling Desertification* vol. 1 (Earthscan Publication Ltd, 2013).
56. Grégoire, C. *et al.* Discovery of a multigene family of aquaporin silicon transporters in the primitive plant *Equisetum arvense*. *Plant J.* **72**, 320–330 (2012).
57. Guerriero, G., Hausman, J. F. & Legay, S. Silicon and the plant extracellular matrix. *Frontiers in Plant Science* vol. 7 463 (2016).

58. Guntzer, F., Keller, C. & Meunier, J. D. Benefits of plant silicon for crops: A review. *Agronomy for Sustainable Development* vol. 32 201–213 (2011).
59. Guo, D. L., Mitchell, R. J. & Hendricks, J. J. Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. *Oecologia* **140**, 450–457 (2004).
60. Hans Wedepohl, K. The composition of the continental crust. *Geochim. Cosmochim. Acta* **59**, 1217–1232 (1995).
61. Harrington, S. *GROWING RICE UNDER CONTROLLED CONDITIONS*. <http://www.ledcome.com/faq.htm> (2010).
62. Haynes, R. J. A contemporary overview of silicon availability in agricultural soils. *Journal of Plant Nutrition and Soil Science* vol. 177 831–844 (2014).
63. Holdaway, R. J., Richardson, S. J., Dickie, I. A., Peltzer, D. A. & Coomes, D. A. Species- and community-level patterns in fine root traits along a 120000-year soil chronosequence in temperate rain forest. *J. Ecol.* **99**, 954–963 (2011).
64. Huang, J. *et al.* Dryland climate change: Recent progress and challenges. *Rev. Geophys.* **55**, 719–778 (2017).
65. Iler, R. K. The chemistry of silica: solubility, polymerization, colloid and surface properties, and biochemistry. *Lavoisierfr* 892 pp (1979) doi:10.1002/ange.19800920433.
66. IPCC. *IPCC Special Report on Climate Change and Land: Chapter 4: Land Degradation*. <https://www.ipcc.ch/report/srccl/> (2019).
67. IPCC. *CLIMATE CHANGE 2013: The Physical Science Basis. Working Group I to the Contributions of the Intergovernmental Panel on Climate Change*. (2013).
68. IRRI, (International Rice Research Institute). *Standard Evaluation System for Rice (SES)*. (2002).
69. ISSS *et al.* *Terminology for soil erosion and conservation*. (1996).
70. Jagadish, K. S. V., Cairns, J. E., Kumar, A., Somayanda, I. M. & Craufurd, P. Q. Does susceptibility to heat stress confound screening for drought tolerance in rice? *Functional Plant Biology* vol. 38 261–269 (2011).
71. Jian, F. M. *et al.* A silicon transporter in rice. *Nature* **440**, 688–691 (2006).
72. Johansson, E., Oscarson, P. & Lundborg, T. Effect of planting date on flowering time in wheat. *Physiol. Plant.* **96**, 338–341 (1996).
73. Johnson, S. N. & Hartley, S. E. Elevated carbon dioxide and warming impact silicon and phenolic-based defences differently in native and exotic grasses. *Glob. Chang. Biol.* 1–11 (2017) doi:10.1111/gcb.13971.

74. Johnson, S. N. *et al.* Climate warming and plant biomechanical defences : Silicon addition contributes to herbivore suppression in a pasture grass. *Funct. Ecol.* 1–10 (2019) doi:10.1111/1365-2435.13295.
75. Jones, M. M. & Turner, N. C. *Osmotic Adjustment in Leaves of Sorghum in Response to Water Deficits I.* *Plant Physiol* www.plantphysiol.org (1978).
76. Kalala, A., Amuri, N. & Semoka, J. Response of Rice to Phosphorus and Potassium Fertilization Based on Nutrient Critical Levels in Plants and Soils of Kilombero Valley. *Adv. Res.* **7**, 1–12 (2016).
77. Katz, O. Silicon content is a plant functional trait: implications in a changing world. *Flora: Morphology, Distribution, Functional Ecology of Plants* vol. 254 88–94 (2019).
78. Kellner, K., Risoli, C. & Metz, M. Terminal Evaluation of the UNEP / FAO / GEF Project “ Land Degradation Assessment in Drylands (LADA)”. *Lada* 118 (2011).
79. Koch, A. *et al.* Soil Security: Solving the Global Soil Crisis. *Glob. Policy* **4**, 434–441 (2013).
80. Köhl, K. Growing rice in controlled environments. *Ann. Appl. Biol.* **167**, 157–177 (2015).
81. Koud, J.-M., Colin, F., Meunier, J.-D. & Alexandre, A. Plant impact on the biogeochemical cycle of silicon and related weathering processes. *Geochim. Cosmochim. Acta* **61**, 677–682 (1997).
82. Krishnan, P., Swain, D. K., Chandra Bhaskar, B., Nayak, S. K. & Dash, R. N. Impact of elevated CO₂ and temperature on rice yield and methods of adaptation as evaluated by crop simulation studies. *Agric. Ecosyst. Environ.* **122**, 233–242 (2007).
83. L.E. Datnoff, G.H. Snyder, G. H. K. *Silicon in Agriculture - Google Books.* (2001).
84. Laliberté, E. Below-ground frontiers in trait-based plant ecology. *New Phytol.* **213**, 1597–1603 (2017).
85. Li, Z., Song, Z. & Cornelis, J. T. Impact of rice cultivar and organ on elemental composition of phytoliths and the release of bio-available silicon. *Front. Plant Sci.* **5**, (2014).
86. Liang, Y., Nikolic, M., Bélanger, R., Gong, H. & Song, A. *Silicon in Agriculture. Silicon in Agriculture* vol. 1 (Elsevier Science Publishers , 2015).
87. Liang, Y., Sun, W., Zhu, Y. G. & Christie, P. Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: A review. *Environ. Pollut.* **147**, 422–428 (2007).
88. Lu, Y. *et al.* Coupled carbon and silicon cycling and characteristics in a subtropical watershed, China. *Ecol. Indic.* **110**, 105897 (2020).

89. Lux, A., Luxová, M., Morita, S., Abe, J. & Inanaga, S. Endodermal silicification in developing seminal roots of lowland and upland cultivars of rice (*Oryza sativa* L.) . *Can. J. Bot.* **77**, 955–960 (1999).
90. Ma, J. F. & Yamaji, N. Functions and transport of silicon in plants. *Cellular and Molecular Life Sciences* vol. 65 3049–3057 (2008).
91. Ma, J. F. & Takahashi, E. *Soil, Fertilizer, and Plant Silicon Research in Japan. Soil, Fertilizer, and Plant Silicon Research in Japan* (2002). doi:10.1016/b978-0-444-51166-9.x5000-3.
92. Ma, J. F. *et al.* A silicon transporter in rice. *Nature* **440**, 688–691 (2006).
93. Ma, J. F. & Yamaji, N. Silicon uptake and accumulation in higher plants. *Trends in Plant Science* vol. 11 392–397 (2006).
94. Ma, J. F. & Yamaji, N. A cooperative system of silicon transport in plants. *Trends in Plant Science* vol. 20 435–442 (2015).
95. Maiti, D., Toppo, N. N. & Variar, M. Integration of crop rotation and arbuscular mycorrhiza (AM) inoculum application for enhancing AM activity to improve phosphorus nutrition and yield of upland rice (*Oryza sativa* L.). *Mycorrhiza* **21**, 659–667 (2011).
96. Makabe, S. *et al.* Relationship between mineral composition or soil texture and available silicon in alluvial paddy soils on the Shounai Plain, Japan. *Soil Sci. Plant Nutr.* **55**, 300–308 (2009).
97. Matichenkov, V. V. & Bocharnikova, E. A. Chapter 13 The relationship between silicon and soil physical and chemical properties. *Stud. Plant Sci.* **8**, 209–219 (2001).
98. McGinnity, P. Silicon and Its Role in Crop Production. 27 (2015).
99. McKeague, J. A. & Cline, M. G. SILICA IN SOIL SOLUTIONS: II. THE ADSORPTION OF MONOSILICIC ACID BY SOIL AND BY OTHER SUBSTANCES. *Can. J. Soil Sci.* **43**, 83–96 (1963).
100. MENGE, J. A., STEIRLE, D., BAGYARAJ, D. J., JOHNSON, E. L. V. & LEONARD, R. T. PHOSPHORUS CONCENTRATIONS IN PLANTS RESPONSIBLE FOR INHIBITION OF MYCORRHIZAL INFECTION. *New Phytol.* **80**, 575–578 (1978).
101. Ming, D. F., Pei, Z. F., Naeem, M. S., Gong, H. J. & Zhou, W. J. Silicon Alleviates PEG-Induced Water-Deficit Stress in Upland Rice Seedlings by Enhancing Osmotic Adjustment. *J. Agron. Crop Sci.* **198**, 14–26 (2012).
102. Mitani, N., Chiba, Y., Yamaji, N. & Ma, J. F. Identification and characterization of maize and barley Lsi2-like silicon efflux transporters reveals a distinct silicon uptake system from that in rice. *Plant Cell* **21**, 2133–2142 (2009).

103. Mitani, N., Yamaji, N., Ago, Y., Iwasaki, K. & Ma, J. F. Isolation and functional characterization of an influx silicon transporter in two pumpkin cultivars contrasting in silicon accumulation. *Plant J.* **66**, 231–240 (2011).
104. Mittler, R. Abiotic stress, the field environment and stress combination. *Trends Plant Sci.* **11**, 15–19 (2006).
105. Mittler, R. & Blumwald, E. Genetic Engineering for Modern Agriculture: Challenges and Perspectives. *Annu. Rev. Plant Biol.* **61**, 443–462 (2010).
106. Mohd Razali, N. & Bee Wah, Y. *Power comparisons of Shapiro-Wilk, Kolmogorov-Smirnov, Lilliefors and Anderson-Darling tests.* *Journal of Statistical Modeling and Analytics* vol. 2 (2011).
107. Montpetit, J. *et al.* Cloning, functional characterization and heterologous expression of TaLsi1, a wheat silicon transporter gene. *Plant Mol. Biol.* **79**, 35–46 (2012).
108. Morita, S. & Nemoto, K. Morphology and anatomy of rice roots with special reference to coordination in organo- and histogenesis. in *Structure and Function of Roots* 75–86 (Springer Netherlands, 1995). doi:10.1007/978-94-017-3101-0_9.
109. Muthayya, S., Sugimoto, J. D., Montgomery, S. & Maberly, G. F. An overview of global rice production, supply, trade, and consumption. *Ann. N. Y. Acad. Sci.* **1324**, 7–14 (2014).
110. Nascimento, A. M., Assis, F. A., Moraes, J. C. & Souza, B. H. S. Silicon application promotes rice growth and negatively affects development of *Spodoptera frugiperda* (J. E. Smith). *J. Appl. Entomol.* 241–249 (2017) doi:10.1111/jen.12461.
111. Nicholson, S. E. Desertification. in *Dryland Climatology* 431–447 (Cambridge University Press, 1998). doi:10.1017/CBO9780511973840.028.
112. Niinemets, Ü. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**, 453–469 (2001).
113. Oh-e, I., Saitoh, K. & Kuroda, T. Effects of high temperature on growth, yield and dry-matter production of rice grown in the paddy field. *Plant Prod. Sci.* **10**, 412–422 (2007).
114. Omasa, K. *et al.* Effects of Elevated CO₂ and Global Climate Change on Rice Yield in Japan. in *Climate Change and Plants in East Asia* 39–56 (Springer Japan, 1996). doi:10.1007/978-4-431-66899-2_4.
115. Oye Anda, C. C., Opfergelt, S. & Declerck, S. Silicon acquisition by bananas (c.V. Grande Naine) is increased in presence of the arbuscular mycorrhizal fungus *Rhizophagus irregularis* MUCL 41833. *Plant Soil* **409**, 77–85 (2016).
116. Parent, B., Suard, B., Serraj, R. & Tardieu, F. Rice leaf growth and water potential are resilient to evaporative demand and soil water deficit once the effects of root system are neutralized. *Plant, Cell Environ.* **33**, 1256–1267 (2010).

117. Peng, S. *et al.* Rice yields decline with higher night temperature from global warming. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 9971–9975 (2004).
118. Pérez-Harguindeguy, N. *et al.* New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **61**, 167–234 (2013).
119. Peterson, G., Allen, C. R. & Holling, C. S. Ecological Resilience, Biodiversity, and Scale. *Ecosystems* **1**, 6–18 (1998).
120. Pimentel, D. & Pimentel, M. Comment: Adverse Environmental Consequences of the Green Revolution. *Popul. Dev. Rev.* **16**, 329 (1990).
121. Pingali, P. L. Green revolution: Impacts, limits, and the path ahead. *Proceedings of the National Academy of Sciences of the United States of America* vol. 109 12302–12308 (2012).
122. Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J. & Villar, R. Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist* vol. 182 565–588 (2009).
123. Prieto, I. *et al.* Root functional parameters along a land-use gradient: Evidence of a community-level economics spectrum. *J. Ecol.* **103**, 361–373 (2015).
124. Rang, Z. W., Jagadish, S. V. K., Zhou, Q. M., Craufurd, P. Q. & Heuer, S. Effect of high temperature and water stress on pollen germination and spikelet fertility in rice. *Environ. Exp. Bot.* **70**, 58–65 (2011).
125. Rapport, D. J., Whitford, W. G. & Hildén, M. Common patterns of ecosystem breakdown under stress. in *Environmental Monitoring and Assessment* vol. 51 171–178 (Kluwer Academic Publishers, 1998).
126. Raven, J. A. Chapter 3 Silicon transport at the cell and tissue level. *Stud. Plant Sci.* **8**, 41–55 (2001).
127. Redman, R. S. *et al.* Increased fitness of rice plants to abiotic stress via habitat adapted symbiosis: A strategy for mitigating impacts of climate change. *PLoS One* **6**, e14823 (2011).
128. Reynolds, J. F. *et al.* Ecology: Global desertification: Building a science for dryland development. *Science* vol. 316 847–851 (2007).
129. Reynolds, O. L., Keeping, M. G. & Meyer, J. H. Silicon-augmented resistance of plants to herbivorous insects: A review. *Ann. Appl. Biol.* **155**, 171–186 (2009).
130. Rodrigues, F. A. & Datnoff, L. E. *Silicon and plant diseases. Silicon and Plant Diseases* (Springer International Publishing, 2015). doi:10.1007/978-3-319-22930-0.
131. Rodriguez, R. J. *et al.* Stress tolerance in plants via habitat-adapted symbiosis. *ISME J.* **2**, 404–416 (2008).

132. Ruíz-Sánchez, M. *et al.* Azospirillum and arbuscular mycorrhizal colonization enhance rice growth and physiological traits under well-watered and drought conditions. *J. Plant Physiol.* **168**, 1031–1037 (2011).
133. Sauer, D., Saccone, L., Conley, D. J., Herrmann, L. & Sommer, M. Review of methodologies for extracting plant-available and amorphous Si from soils and aquatic sediments. *Biogeochemistry* vol. 80 89–108 (2006).
134. Savant, N. K., Snyder, G. H. & Datnoff, L. E. Silicon Management and Sustainable Rice Production. *Adv. Agron.* **58**, 151–199 (1996).
135. Sherwood, S. & Fu, Q. A drier future? *Science (80-.)*. **343**, 737–739 (2014).
136. Shukla, A., Kumar, A., Jha, A., Ajit & Rao, D. V. K. N. Phosphorus threshold for arbuscular mycorrhizal colonization of crops and tree seedlings. *Biol. Fertil. Soils* **48**, 109–116 (2012).
137. Singh, R. B. Environmental consequences of agricultural development: A case study from the green revolution state of Haryana, India. *Agric. Ecosyst. Environ.* **82**, 97–103 (2000).
138. Sistani, K. R., Savant, N. K. & Reddy, K. C. Effect of rice hull ash silicon on rice seedling growth. *J. Plant Nutr.* **20**, 195–201 (1997).
139. Sommer, M., Kaczorek, D., Kuzyakov, Y. & Breuer, J. Silicon pools and fluxes in soils and landscapes - A review. *Journal of Plant Nutrition and Soil Science* vol. 169 310–329 (2006).
140. Song, Z., Müller, K. & Wang, H. Biogeochemical silicon cycle and carbon sequestration in agricultural ecosystems. *Earth-Science Reviews* vol. 139 268–278 (2014).
141. Street-Perrott, F. A. & Barker, P. A. Biogenic silica: A neglected component of the coupled global continental biogeochemical cycles of carbon and silicon. *Earth Surf. Process. Landforms* **33**, 1436–1457 (2008).
142. Suzuki, N., Rivero, R. M., Shulaev, V., Blumwald, E. & Mittler, R. Abiotic and biotic stress combinations. *New Phytol.* **203**, 32–43 (2014).
143. Suzuki, S. *et al.* Silicon deficiency promotes lignin accumulation in rice. *Plant Biotechnol.* **29**, 391–394 (2012).
144. Tavakkoli, E., Lyons, G., English, P. & Guppy, C. N. Silicon nutrition of rice is affected by soil pH, weathering and silicon fertilisation. *J. Plant Nutr. Soil Sci.* **174**, 437–446 (2011).
145. Taylor, L. L. *et al.* Biological weathering and the long-term carbon cycle: Integrating mycorrhizal evolution and function into the current paradigm. *Geobiology* **7**, 171–191 (2009).

146. Thiaw, I. Soil and the SDGs: challenges and need for action. in *Executive Secretary of the UNCCD 13–14* (European Commission, Directorate General for Environment (DG ENV), 2019).
147. Tinus, R. W. Root growth potential as an indicator of drought stress history. *Tree Physiol.* **16**, 795–799 (1996).
148. Tréguer, P. & Pondaven, P. Silica control of carbon dioxide. *Nature* vol. 406 358–359 (2000).
149. Tubaña, B. S. & Heckman, J. R. Silicon in soils and plants. in *Silicon and Plant Diseases 7–51* (Springer International Publishing, 2015). doi:10.1007/978-3-319-22930-0_2.
150. UNCCD. *The Global Land Outlook, first edition.* (2017). doi:ISBN: 978-92-95110-48-9.
151. Van Bockhaven, J., De Vleeschauwer, D. & Höfte, M. Towards establishing broad-spectrum disease resistance in plants: silicon leads the way. *Journal of experimental botany* vol. 64 1281–1293 (2013).
152. Vandegeer, R. K., Tissue, D. T., Hartley, S. E., Glauser, G. & Johnson, S. N. Physiological acclimation of a grass species occurs during sustained but not repeated drought events. *Environ. Exp. Bot.* **171**, (2020).
153. VERBRUGGEN, E., Van Der HEIJDEN, M. G. A., WEEDON, J. T., KOWALCHUK, G. A. & RÖLING, W. F. M. Community assembly, species richness and nestedness of
154. Vierheilig, H. Regulatory mechanisms during the plant - Arbuscular mycorrhizal fungus interaction. in *Canadian Journal of Botany* vol. 82 1166–1176 (2004).
155. Vierheilig, H., Coughlan, A. P., Wyss, U. & Piché, Y. *Ink and Vinegar, a Simple Staining Technique for Arbuscular-Mycorrhizal Fungi.* *APPLIED AND ENVIRONMENTAL MICROBIOLOGY* vol. 64 <http://aem.asm.org/> (1998).
156. Vivancos, J., Labbé, C., Menzies, J. G. & Bélanger, R. R. Silicon-mediated resistance of Arabidopsis against powdery mildew involves mechanisms other than the salicylic acid (SA)-dependent defence pathway. *Mol. Plant Pathol.* **16**, 572–582 (2015).
157. Voinovitch, I. A., Debras-Guedon, J. & Louvrier, J. L'analyse des silicates. in 145–158 (1962).
158. Wang, Y., Stass, A. & Horst, W. J. Apoplastic binding of aluminum is involved in silicon-induced amelioration of aluminum toxicity in maize. *Plant Physiol.* **136**, 3762–3770 (2004).
159. Wassmann, R. *et al.* Chapter 3 Regional Vulnerability of Climate Change Impacts on Asian Rice Production and Scope for Adaptation. *Advances in Agronomy* vol. 102 91–133 (2009).

160. Welch, J. R. *et al.* Rice yields in tropical/subtropical Asia exhibit large but opposing sensitivities to minimum and maximum temperatures. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 14562–14567 (2010).
161. Welch, J. R. *et al.* Rice yields in tropical/subtropical Asia exhibit large but opposing sensitivities to minimum and maximum temperatures. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 14562–14567 (2010).
162. Winslow, M., Shapiro, B. I., Thomas, R. & Shetty, S. V. R. Desertification , Drought , Poverty and Agriculture : Research Lessons and Opportunities. *Icrisat/Icarda/Unccd Gm 52* (2004).
163. Wopereis, M. C. S., Kropff, M. J., Maligaya, A. R. & Tuong, T. P. Drought-stress responses of two lowland rice cultivars to soil water status. *F. Crop. Res.* **46**, 21–39 (1996).
164. Wynn Owen, P. Combating desertification in the European Union. in *Conference ‘Soil and the SDGs: challenges and need for action’* (ed. Wageningen Environmental Research and Deltares) 19–21 (European Commission, DG Environment., 2019).
165. Yahara, H., Tanikawa, N., Okamoto, M. & Makita, N. Characterizing fine-root traits by species phylogeny and microbial symbiosis in 11 co-existing woody species. *Oecologia* **191**, 983–993 (2019).
166. Yost, R. S. & Fox, R. L. Influence of Mycorrhizae on the Mineral Contents of Cowpea and Soybean Grown in an Oxisol 1. *Agron. J.* **74**, 475–481 (1982).
167. Zañão, L. A., Fontes, R. L. F., Neves, J. C. L., Korndörfer, G. H. & de Ávila, V. T. Rice grown in nutrient solution with doses of manganese and silicon. *Rev. Bras. Cienc. do Solo* **34**, 1629–1639 (2010).
168. Zandalinas, S. I., Mittler, R., Balfagón, D., Arbona, V. & Gómez-Cadenas, A. Plant adaptations to the combination of drought and high temperatures. *Physiol. Plant.* **162**, 2–12 (2018).
169. Zdruli, P., Lal, R., Cherlet, M. & Kapur, S. New World Atlas of Desertification and Issues of Carbon Sequestration, Organic Carbon Stocks, Nutrient Depletion and Implications for Food Security. in *The Anthropocene: Politik–Economics–Society–Science* 13–25 (2017). doi:10.1007/978-3-319-45035-3_2.
170. Zhang, C., Wang, L. & Zhang, W. Do lignification and silicification of the cell wall precede silicon deposition in the silica cell of the rice (*Oryza sativa* L .) leaf epidermis ? *Plant Soil* **372**, 137–149 (2013).
171. Zhao, C. *et al.* Temperature increase reduces global yields of major crops in four independent estimates. *Proc. Natl. Acad. Sci. U. S. A.* **114**, 9326–9331 (2017).
172. Zhou, H. *et al.* Environmental explanation of maize specific leaf area under varying water stress regimes. (2019) doi:10.1016/j.envexpbot.2019.103932.

173. Ziska, L. H., Namuco, O., Moya, T. & Quilang, J. Growth and Yield Response of Field-Grown Tropical Rice to Increasing Carbon Dioxide and Air Temperature. *Agron. J.* **89**, 45–53 (1997).