Estimating oil-palm Si storage, Si return to soils and Si losses through harvest in smallholder oil-palm plantations of Sumatra, Indonesia

Britta Greenshields[1], Barbara von der Lühe[1], Felix Schwarz[1], Harold J. Hughes[1], Aiyen Tjoa[2], Martyna Kotowska[3], Fabian Brambach[4], Daniela Sauer[1]

[1]Department of Physical Geography, University of Göttingen, Göttingen, Germany
[2]Faculty of Agriculture, Tadulako University, Palu, Indonesia
[3]Department of Plant Ecology and Ecosystems Research, University of Göttingen, Göttingen, Germany
[4]Department of Biodiversity, Macroecology & Biogeography, University of Göttingen, Göttingen, Germany

Correspondence to: Britta Greenshields (britta.greenshields@uni-geottingen.de)

Abstract. ~~Silicon (Si) is known to have multiple beneficial effects on crops.~~ Most plant-available Si in strongly desilicated soils is provided through litter decomposition and subsequent phytolith dissolution.~~, especially in strongly desilicated tropical soils.~~ The importance of Si cycling in tropical soil-plant systems raised the question if oil-palm cultivation~~, the oil palm being a Si-accumulating crop,~~ alters Si cycling. As ~~Si accumulates in plant tissue~~oil palms are considered Si hyper-accumulators, we hypothesized that ~~i)~~much Si is stored in the aboveground biomass of oil palms with time.~~, and that ii)~~Furthermore, the system might lose considerable amounts of Si every year through fruit-bunch harvest. To test these hypotheses, we analysed Si concentrations in fruit-bunch stalks, fruit pulp and kernels, as well as in ~~sampled~~ leaflets, ~~the~~ rachises, ~~fruit-bunch stalk~~and ~~, fruit pulp, kernels and~~ frond bases ~~from~~ of mature oil palms ~~planted on well-drained and temporarily flooded riparian~~on eight smallholder oil-palm plantations ~~(n = 4 each)~~ in ~~lowland~~ Sumatra, Indonesia. We ~~quantified Si concentrations of these oil-palm parts by $NaCO_3$-extraction. We further~~ estimated Si storage in the total above-ground biomass of ~~the~~ oil palms, Si return to soils through decomposing pruned palm fronds, and Si losses from the system through harvest.~~, to assess if Si return to soils via pruned palm fronds sufficed for maintaining Si cycling in the system, or if any measures are needed to compensate for Si export through fruit-bunch harvest. At all sites, L~~Leaflets of oil-palm fronds had a ~~significantly higher ($p \leq 0.05$)~~ mean Si concentration ~~(~~≥~~≥~~ 1 wt. %.~~)~~ All other analysed plant parts had < 0.5 wt. % Si. According to our estimates, ~~than the rachis, frond base, fruit-bunch stalk, fruit pulp and kernel (≤ 0.5 wt. %). All analysed oil-palm parts had a Si/Ca weight ratio ≥ 1, except for the rachis. At well-drained sites, mean Si concentrations in leaflets increased with palm-frond age (R^2 = 0.98). Estimates of Si storage in the total above-ground biomass of oil palms, Si return to soils through decomposing pruned palm fronds, and Si losses through harvest were similar at well-drained and riparian sites:~~ a single palm tree ~~could~~ stored about 4 – 5 kg ~~of~~ Si in its total above-ground biomass.~~,~~ A~~a~~ smallholder oil-palm plantation ~~of 1 hectare could~~ stored ~~about~~ at least 550 kg ~~of~~ Si per hectare in the palm trees' above-ground biomass. Pruned palm fronds ~~were estimated to~~ returned 111~~0~~ – 131 kg of Si per hectare to topsoils each year. Fruit-bunch harvest corresponded to an annual Si export of 32 – 72 kg Si per hectare in 2015 and 2018. ~~Thus, on smallholder plantations in our study area, more Si can be returned to soils through pruned palm fronds than is lost through fruit-bunch harvest.~~ Greater Si losses (of at least 550 kg Si per hectare) would occur from the system if oil-palm stems were removed from plantations prior to replanting. Therefore, it is advisable to leave oil-palm stems on the plantations e.g., by distributing chipped stem parts across the plantation at the end of a plantation cycle (~25 years). ~~This would return about 550 kg ha^{-1} Si stored in the palm trees' above-ground biomass to the soils.~~

Keywords: oil-palm management, silicon cycling, silicon balance, silicon export through harvest, tropical soils

1 Introduction

Indonesia has become one of the largest global palm-oil producers with currently ~16 million ha under oil-palm cultivation (Gaveau et al., 2022). In the 1980s, the emerging palm-oil boom led to clearing of rainforests (Tsujino et al., 2016; Qaim et al., 2020). Since then, palm oil has remained a tropical cash crop with high demand on the global market (Qaim et al., 2020) due to its versatile use, e.g., as vegetable oil, in cosmetics, and biofuels (FAO

2020). In Jambi Province, Indonesia, oil-palm cultivation has improved the livelihoods of many smallholder farmers, yet at the expense of the natural environment (Clough et al., 2016; Grass et al., 2020; Qaim et al., 2020). This has resulted in a decrease in biodiversity (Drescher et al., 2016; Meijaard et al., 2020) and ecosystem services (Dislich et al., 2017). To balance ecosystem preservation (Tsujino et al., 2016) and economic prosperity (Grass et al., 2020), current research aims to identify ways to increase land-use sustainability while keeping current oil-palm plantations profitable (Darras et al., 2019; Luke et al., 2019).

Oil palms, like many other crops, ~~are economically important tropical crops (Qaim et al., 2020). They~~ are commonly grown on highly weathered soils that have been exposed to intense element leaching, including phosphorous (P), potassium (K), calcium (Ca) and silicon (Si) (Haynes, 2014). ~~(Haynes, 2014).~~ Yet, well-balanced Si levels in soils are essential for many crops~~,~~ ~~as~~ because Si can ~~has several beneficial effects on crops, e.g.,~~ promote~~ing~~ the release of adsorbed macro-nutrients and prevent~~ing~~ plant toxicity at low soil pH (Epstein, 2009). Plants store Si in their leaf tissue~~. It strengthens their tissue, in this way~~to mitigate~~ing~~ biotic and abiotic stresses and to reduce~~ing~~ transpiration. ~~Plants take up~~ Si is taken up from soil solution as monomeric silicic acid (H_4SiO_4) (Haynes, 2017) and ~~. Si is~~ then transported from the roots to the shoot with the ~~sap~~ xylem flow (Liang et al., 2015). Transpiration ~~leads to an~~ increases the~~ir~~ Si concentration in the leaf tissue, ~~and~~ where ~~finally~~ Si finally precipitates as amorphous silica bodies called phytoliths ($SiO_2 * nH_2O$) (Liang et al., 2015; Haynes, 2017). It preferentially precipitates in epidermal cell walls, the cell lumen, and intercellular spaces of any plant part, such as the shoot, leaflets, leaf stalk, and fruit (Liang et al., 2015). Si can also precipitate in certain Si cells associated with the vascular system in the stem or endodermis of roots (Epstein, 1994; Haynes, 2017).

Plants can be grouped into three categories based on the Si concentration and Si/Ca ratio in their dry leaf tissue (Ma and Takahashi, 2002): (I) non-accumulators or excluders (Si concentration < 0.5 wt. %; Si/Ca < 0.5); (II) intermediate accumulators (Si concentration 0.5 – 1 wt. %; Si/Ca 0.5 – 1) and (III) accumulators (Si concentration > 1 wt. %; Si/Ca > 1). To better distinguish between plants of groups II and III, we will use the term "hyper-accumulator" for plants of group III throughout this paper. Following this terminology, Si hyper-accumulators include~~Several crops are classified as Si accumulators,~~ e.g., rice (*Oryza sativa* L.), barley (*Hordeum vulgare* L.), maize (*Zea mays* L.), wheat (*Triticum aestivum* L.) and sugarcane (*Saccharum officinarum* L.) (Haynes, 2017). According to ~~These Si accumulators share the following characteristics: (i) taking up Si either actively or passively from soil solution (Haynes, 2017; Liang et al., 2015), (ii) accumulating at least 1 wt. % Si based on dry weight in their leaf tissue and having a Si/Ca ratio of at least 1 (Ma and Takahashi, 2002), (iii) reaching similar concentration levels as macro-nutrients (Haynes, 2017), and (iv) Si remaining immobile in plant tissue .~~ Munevar and Romero (2015), ~~-~~oil palms are Si hyper-accumulators, too. They reported high Si concentrations in oil-palm fronds in Colombia~~, suggesting that oil palms are Si-accumulating plants, too. They quantified Si concentrations in oil-palm leaves of various ages~~ and found that the Si concentration increased with leaf age.~~,~~ ~~concluding Si remained immobile in plant tissue.~~ However, these observations have not yet been confirmed in any other oil-palm growing region~~, like South-East Asia or West Africa~~. In addition, Si concentrations of oil-palm parts other than leaves need to be quantified to reliably estimate Si storage in oil palms.

~~-~~Several studies have shown that land conversion from forests to arable land has caused soil Si depletion on the long term (Struyf et al., 2010; Clymans et al., 2015; Carey and Fulweiler, 2016). Thereby, reduced Si return to soils through litter input and Si export through crop harvest were identified as main drivers (Puppe et al., 2021;

Vandevenne et al., 2012; Guntzer et al., 2012). The weathering stage of soils ~~which~~ can also affect biological Si cycling (vander Linden and Delvaux, 2019; Carey, 2020; de Tombeur et al., 2020). In strongly weathered soils, Si cycling is predominantly maintained by the recycling of phytoliths (de Tombeur et al., 2020). For these reasons, some crops already receive Si fertilizers, especially when cultivated on strongly weathered, naturally desilicated soils (Datnoff et al., 1997; Li and Delvaux, 2019; Zellner et al., 2021). Under oil-palm plantations, amorphous Si concentrations in topsoil were decreased (by factor 1.25) compared to rainforest topsoil (von der Lühe et al., 2020). Furthermore, the dissolution rate of phytoliths isolated from oil-palm litter was significantly lower compared to rainforest litter (von der Lühe et al., 2022). These previous observations suggest that rainforest conversion to oil-palm plantations can considerably alter Si cycling.

~~The data of Munevar and Romero (2015) suggested that oil palms belong to the Si-accumulating crops.~~ This raised our concern that oil-palm cultivation may lead to soil Si depletion ~~over~~ with time, to a degree that could negatively affect future crop yields.~~,~~

~~motivating us to carry out this study. We quantified key Si pools and fluxes in oil-palm plantations, which was done for the first time. Our study was based on the assumption that~~ Si cycling differs between ~~in~~ oil-palm plantations ~~differs from that in~~and undisturbed terrestrial ecosystems: in undisturbed terrestrial ecosystems,~~,~~ ~~where plant-available Si pools in soils are continuously replenished, as~~ Si returns to soil through litterfall. Subsequent litter decomposition leads to an accumulation of phytoliths in the topsoil (Conley et al., 2008; Li et al., 2020), which is a key source of Si that can easily become plant-available (Lucas et al., 1993; Alexandre et al., 1997; Schaller et al., 2018). In oil-palm plantations, Si which has been taken up by oil palms mainly returns to soils through decomposing palm fronds (von der Lühe et al., 2022) which are pruned and then commonly stacked in piles in every second row of a plantation (Dislich et al., 2017). Phytolith accumulation in topsoils is therefore largely restricted to frond pile areas (Greenshields et al., 2022; von der Lühe et al., 2022) which may comprise as little as ~12 % of a plantation (Tarigan et al., 2020). In oil-palm plantations, ~~however, we expected~~ Si cycling is expected to be further disrupted by fruit-bunch harvest. ~~return from plants to soil to be disrupted, as palm fronds are cut-off and stacked in piles (Dislich et al., 2017). Thus, we hypothesised that Si return to soil from pruned palm fronds does not take place equally across a plantation, but is largely restricted to frond piles, leading to a heterogenous spatial pattern of phytoliths within a plantation. In addition, we considered~~ Si losses from the system can be considerable~~through harvest,~~ as not only fruit, but entire fruit bunches are removed from the system (Kotowska et al., 2015; Euler et al., 2016a). Lastly, oil palms have a ~25-year cultivation cycle (Corley and Tinker, 2016). Many oil-palm plantations in Indonesia are currently approaching the end of their first cultivation cycle in Sumatra. Yet, there is no clear strategy~~,~~ on how to use the biomass of the first-generation oil palms (Awalludin et al., 2015).

To our knowledge, only Munevar and Romero (2015) have quantified Si concentrations in oil-palm leaves so far. ~~Yet quantitative Si data for Indonesia, one of the largest global palm-oil producers with ~16 million ha under oil-palm cultivation, is missing (Gaveau et al., 2022).~~ Furthermore, no ~~studies analysing~~ Si concentrations from oil-palm parts other than leaflets have been reported yet. Therefore, our study in a region dominated by smallholder oil-palm plantations in lowland Sumatra, Indonesia, had two aims: first, to test whether oil palms in Indonesia can be considered Si hyper-accumulators, and second, to estimate Si storage in oil palms, Si losses from the system through harvest, and Si return from plants to soils on ~~these~~ oil-palm plantations. ~~. Thereby, we expected that soils~~

~~in low lying riparian areas might be less affected by Si depletion than soils in higher landscape positions for the following reasons: by potentially receiving dissolved silicic acid through lateral water fluxes (interflow) from higher lying areas, where soil Si is leached, as well as through flooding and capillary rise of groundwater~~in two different landscape positions (well-drained areas – slopes; riparian areas – floodplains) and WRB reference soil groups (Acrisols and Stagnosols). We hypothesized that much Si is stored in the aboveground biomass of oil palms with time. Furthermore, the system might lose considerable amounts of Si every year through fruit-bunch harvest. To account for the landscape position, we further hypothesized that soils in riparian areas might be less affected by Si depletion because they additionally receive dissolved silicic acid through flooding and capillary rise of groundwater as well as through lateral water fluxes (inflow) from higher landscape areas. We expected that greater Si availability in riparian areas would result in greater Si uptake, and consequently in greater Si storage in the aboveground biomass of riparian oil-palm plantations.~~.~~

2 Materials and Methods

2.1 Study area and selected oil-palm plantations

The study was conducted in the lowlands of Jambi Province, Sumatra, Indonesia (1° 55' 0'' S, 103° 15' 0'' E; 50 m ± 5 m NN). The region has a humid tropical climate with a mean annual temperature of 26.7 °C and a mean annual precipitation of 2230 mm yr^{-1} (Drescher et al., 2016). The climate is characterised by two rainy seasons in December and March and a dry season lasting from July to August (Drescher et al., 2016). The geological basement of the study area consists of pre-Paleogene metamorphic and igneous bedrock alongside lacustrine and fluvial sediments (de Coster, 2006). The soils in well-drained areas at higher landscape positions are predominantly Acrisols, whereas the temporarily flooded riparian areas are dominated by Stagnosols (IUSS Working Group WRB, 2022; Hennings et al., 2021). The natural vegetation is mixed dipterocarp lowland rainforest (Laumonier, 1997). Alongside oil-palm plantations, large areas in the lowlands of Jambi Province are also covered by rubber, jungle rubber and commercial timber (Dislich et al., 2017). We conducted sampling on smallholder oil-palm plantations (≤ 2 ha) at four well-drained (Acrisols) and four riparian (Stagnosols) sites (Dislich et al., 2017). On each plantation, ~~research~~ study plots (50 x 50 m) were established by the Collaborative Research Centre CRC 990 – EFForTs (funded by the German Research Foundation). At the time of sampling, oil palms were 18 – 22 years old at the well-drained sites (HO1 – 4)~~ were 18 – 22 years old~~, and 11 – 21 years old ~~oil palms~~ at ~~the~~ riparian sites (HOr1 – 4) ~~were 11 – 21 years old~~(Hennings et al., 2021). The average planting density was 142 ± 17 oil palms per hectare. O~~The o~~il palms were planted in a triangular planting array with ~9 m distance between individual palm trees. Smallholder farmers followed common management practices. Thereby, interrows (i.e., empty spaces on either side of ~~the~~ an oil-palm row)~~s~~ either served as harvesting paths or were used to stack pruned palm fronds (Darras et al., 2019). Herbicides (e.g., glyphosate) were sprayed ~~biannually~~ twice per year to clear understory vegetation in the interrows. The palm circle, a circular area with a radius of ca. 2 m around ~~each~~ an oil-palm stem~~, where fertilizer is applied,~~ (Munevar and Romero, 2015), was weeded regularly. Inorganic fertilizers (NPK, KCl and urea) were applied ~~biannually~~ twice per year within the palm circle (Allen et al., 2016; Euler et al., 2016b).

2.2 Study design and plant sampling

We aimed t~~T~~o quantify Si concentrations in the different plant parts of an oil palm~~,~~ and to subsequently derive Si storage estimates for the average total above~~-~~ground biomass of ~~the oil palms~~one hectare of oil-palm plantation. For this purpose, we sampled leaflets, ~~the~~ rachises, fruit-bunch stalks, fruit pulp, ~~the~~ kernels, and frond bases of oil palms (aAppendix, Table A1). Oil-palm sampling was coordinated with the regional harvesting schedule to ensure that all sampled oil-palm parts (n = 3 for each part) originated from the same palm tree. At each well-drained (HO1 – 4) and riparian site (HOr1 – 4), three morphologically similar oil palms carrying with at least one ripe fruit bunch were selected for sampling (aAppendix, Table B2).

The regular phyllotaxis of the oil palm allows to group palm fronds into (i) young fronds, (ii) mature fronds and (iii) senescing fronds (Rees, 1964; Albakri et al., 2019) (Fig. 1a, c, d). Frond no. 1 is the youngest frond, frond no. 9 is the first mature frond, and the senescing frond (~leaf no. 40) the oldest frond still attached to the oil-palm stem (Corley and Tinker, 2016). Grouping fronds according to age is important because we assume that they have different Si concentrations (Munevar and Romero, 2015). Frond no. 17 is commonly used as a reference frond to determine the nutrient status of a palm tree (Ollivier et al., 2017; Amirruddin et al., 2017). We collected leaflets from frond no. 9, frond no. 17 and from a senescing frond. Palm fronds are ranked according to age. Thereby frond no. 1 is the youngest leaf, frond no. 9 is the first mature leaf, and the senescing frond (~leaf no. 40) the oldest frond still attached to the oil-palm stem (Corley and Tinker, 2016). We also sampled the rachises and frond bases (attachment of petiole to the stem). In addition, we sampled a ripe fruit bunch of each selected palm tree. The latter was subdivided into fruit-bunch stalk, fruit pulp and kernel (Fig. 1a). We could did not have the opportunitynot to sample the oil-palm stems (Fig. 1b) and therefore refer used datato of Pratiwi et al. (2018) in our Si storage calculations. They quantified SiO_2 concentrations of oil-palm stems in Malaysia, which we converted into Si concentrations. All Si concentrations are presented as wt. % of the dry biomass of each part. The grand means refer to three oil palms per plot, which provided the basise for subsequent Si storage calculations.

In well-drained areas, we additionally assessed how Si accumulated with leaf age. For this purpose, we sampled leaflets from two additional mature palm fronds, i.e., frond no. 22 and frond no. 25 from two oil palms per plot. To exclude any bias in the calculations of Si accumulation in leaf tissue, the grand means of frond no. 9, no. 17, no. 22, no. 25, and the senescing frond were all calculated based on two oil palms per plot (Tab. 1). Contrary to Munevar and Romero (2015), we only included mature fronds (≥ leaf no. 9). In the field, oil-palm leaflets were wiped clean of dust and then cut into smaller pieces. Fruit were cut-off from the lower part of the fruit bunch. The oil-palm parts were then dried at 60 °C for 48 h. Prior to analysis, leaflets were finely ground (5 min). The rachises, frond bases, and fruit-bunch stalks were first cut into chunks and then chopped finely. Fruit pulp was separated from the kernel. The kernels were cooled with liquid nitrogen so that they could be crushed and ground despite their high oil content. They were then ground into a fine powder in a stainless-steel mortar.

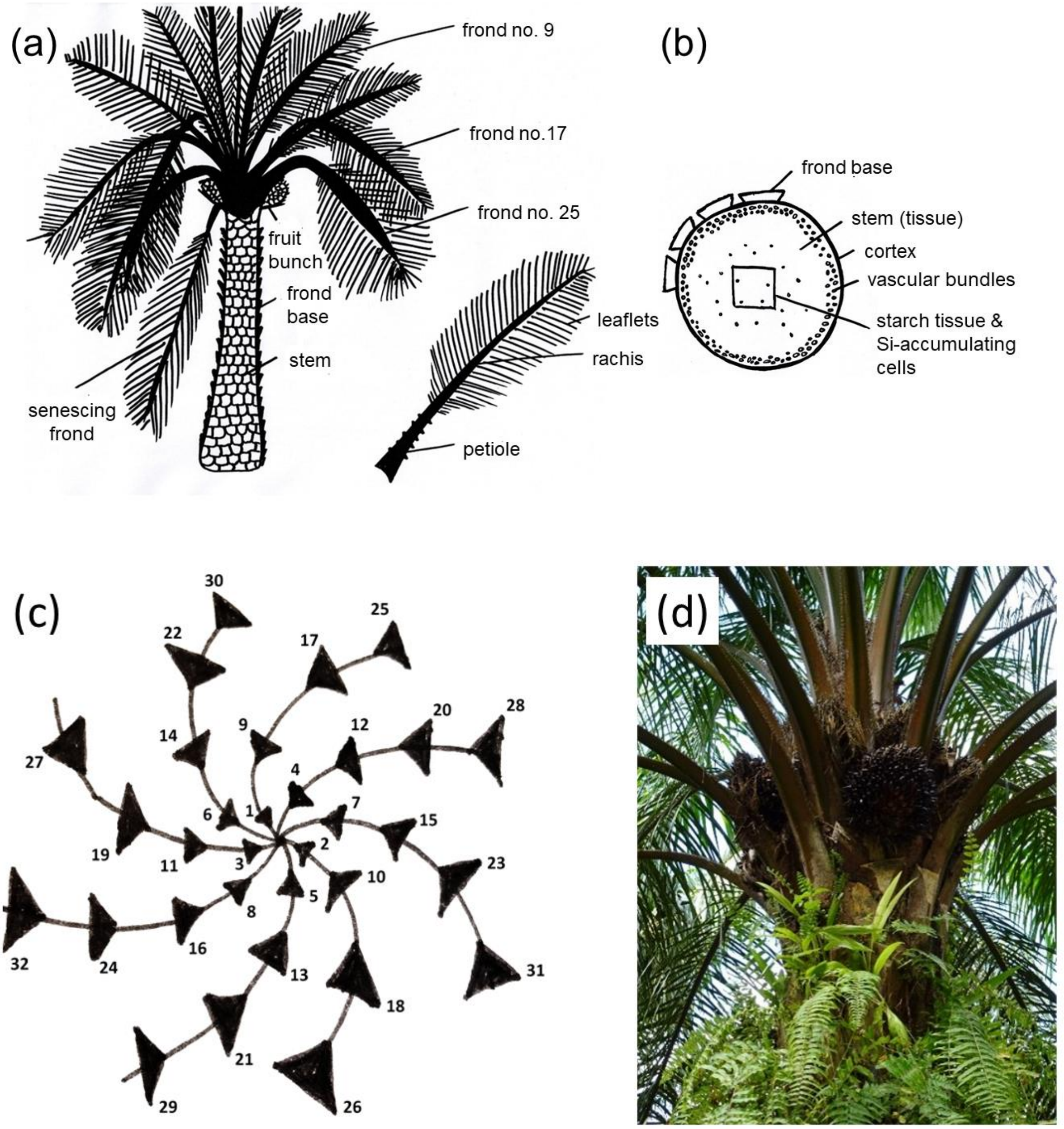

Fig. 1 ~~a~~ ~~Sketch of analysed~~Morphology of the oil palm (*Elaeis guineensis L.*) and ~~oil-palm~~plant parts sampled for this study ~~-~~after Lewis et al. (2020) (a).
~~**Fig. 1b**~~ C~~Sketch of c~~ross-section through an oil-palm stem, including Si-accumulating cells after Dungani et al. (2013) (b). Phyllotaxis of the oil palm after Albakri et al. (2019). Black triangles represent palm fronds (c). Oil-palm crown with regular phyllotaxis (photo, B. Greenshields) (d).

~~In well-drained areas, we additionally assessed how Si accumulated with leaf age. For this purpose, we sampled leaflets of two additional mature palm fronds, frond no. 22 and frond no. 25 from two oil palms per plot. To exclude any bias in the calculations of Si accumulation in leaf tissue, the grand means of frond no. 9, no. 17, no. 22, no. 25, and the senescing frond were all calculated based on two oil palms per plot. Contrary to Munevar and Romero (2015), we only included mature fronds (≥ leaf no. 9). In the field, oil-palm leaflets were wiped clean of dust and then cut into smaller pieces. Fruit were cut-off from the lower part of the fruit bunch. The oil-palm parts were then dried at 60 °C for 48 h. Prior to analysis, leaflets were finely ground (5 min). The rachis, frond bases, and fruit-bunch stalk were first cut into chunks and then chopped finely. Fruit pulp was separated from the kernel. The kernel was cooled with liquid nitrogen to be able to crush and grind it despite its high oil content. It was then ground into a fine powder in a stainless-steel mortar.~~

Table 1 Sampling scheme and numbers of replicates, providing the statistical basis of Figures 2 and 3

Oil-palm part	Water regime[b]	Palm trees (replicates per plot)	Plots (replicates per water regime)	Replicates of palm trees/plots used for Fig. 2	Replicates of palm trees/plots used for Fig. 3
Frond no. 9	WD	3	4	3/4	*2 (excl. palm 3)*/4
Frond no. 17	WD	3	4	3/4	*2 (excl. palm 3)*/4
Senescing frond	WD	3	4	3/4	*2 (excl. palm 3)*/4
Rachis	WD	3	4	3/4	***
Frond base	WD	3	4	3/4	***
Fruit-bunch stalk	WD	3	4	3/4	***
Fruit pulp	WD	3	4	3/4	***
Kernel	WD	3	4	3/4	***
Frond no. 22	WD	*2 (excl. palm 3)*	4	***	*2 (excl. palm 3)*/4
Frond no. 25	WD	*2 (excl. palm 3)*	4	***	*2 (excl. palm 3)*/4
Frond no. 9	RI	3	4	3/4	***
Frond no. 17	RI	3	4	3/4	***
Senescing frond[a]	RI	3	*3 (excl. HOr2)*	3/3	***
Rachis	RI	3	4	3/4	***
Frond base	RI	3	4	3/4	***
Fruit-bunch stalk	RI	3	4	3/4	***
Fruit pulp	RI	3	4	3/4	***
Kernel	RI	3	4	3/4	***

[a] only 3 replicate plots as no senescing fronds were left hanging on palm trees at site HOr2 (differing management practice)
[b] WD = well-drained, RI = riparian / [c] Italics = differing from general sampling scheme / *** = not relevant for statistics.

2.3 Extraction methods

2.3.1 Alkaline extraction for determining Si concentrations of oil-palm parts

Si was extracted from all sampled oil-palm parts by leaching with 1-% Na_2CO_3 after Meunier et al. (2014) and Saccone et al. (2007). As 1% Na_2CO_3 may not completely dissolve amorphous silica (Saccone et al., 2007; Li and Delvaux, 2019), we conducted a pre-test to compare the efficiency of 1 M NaOH and 1% Na_2CO_3 to extract Si from various types of plant parts included in this study. NaOH could generally extract Si more efficiently from those plant parts remaining in the system, whereas Na_2CO_3 could extract Si more efficiently from those parts leaving the system through harvest (except for the fruit-bunch stalk, which underestimated Si by 8%). As the latter are more important for calculating the final Si budget of the system, we decided to use Na_2CO_3. Each plant sample was extracted and analysed in two laboratory replicates. We accepted ≤ 10% relative error between the two laboratory replicates. In case this threshold was exceeded, a third replicate was done.

~~The procedure was conducted on two replicate samples.~~ 40 ml of 1-% Na_2CO_3 solution was added to approximately 50 mg of finely ground plant material in 50 ml centrifugation tubes. The tubes were placed into a shaking hot water bath at 85 °C (continuous shaking, 85 rpm) and were additionally shaken manually after 1 h. The tubes were left to react overnight for 16 hours. On the next day, the samples were cooled off in a cold-water basin for 10 min and were then centrifuged for 5 min at 3000 rpm. An aliquot of 125 µl was transferred into a plastic tube, neutralized with 1125 µl 0.021 M HCl and diluted to 2.5 ml with deionised water. Si was analysed according to the molybdenum blue method (Grasshoff et al., 2009) with a UV-VIS spectrophotometer (Lambda 40, Perkin Elmer, Germany) at 810 nm.

2.3.2 HNO_3 digestion for determining calcium (Ca) concentrations of oil-palm parts

Ca concentrations of all sampled oil-palm parts were determined by HNO_3 digestion (Heinrichs and Hermann, 1990; Heinrichs et al., 1986). Prior to analysis, 50 ml teflon beakers were rinsed with deionised water (18.3 Ω) and dried (60 °C, 24 h). Approximately 50 – 150 mg of sample was weighed into each teflon beaker. Then 2 ml of concentrated HNO_3 solution was added to each sample. The teflon beakers were closed with a teflon lid and inserted into digestion blocks. These digestion blocks were placed into a drying oven and left to react at 170 °C for 10 hours. Afterwards~~Then~~, the digestion solution was transferred into 50 ml volumetric flasks through ash-free filters and filled up with de-ionised water to 50 ml. Ca concentrations were measured with an inductively coupled plasma atomic emission spectrometer (ICP-AES, iCap 7000, Thermo Fisher Scientific GmbH, Germany) at 317.887 nm.

2.4 Estimating Si storage in the above~~-~~ground biomass of oil palms and~~in~~ 1 hectare of plantation

For any given oil-palm part, Si storage can be calculated by multiplying the Si concentration by its dry weight biomass. As we quantified Si concentrations of oil-palm subparts, i.e., leaflets, rachises, frond bases, fruit-bunch stalks, fruit pulp and kernels (Section 2.2, Tab. 2~~1~~a), but literature mostly provided dry weights of oil-palm main parts, i.e., the stem with palm-frond bases, palm fronds, palm crown and fruit bunches (Corley et al., 1971; Lewis et al., 2020), estimating Si storage in the above~~-~~ground biomas of oil-palms and one~~1~~ hectare oil-palm plantation required some additonal calculations as follows: we first estimated the dry biomass of each oil-palm subpart by multiplying the dry biomass of each main part by its percentage contribution of the respective subpart (Tab. 2~~1~~a). We then multiplied the dry biomass of each subpart by its mean Si concentration (Tab. 2~~1~~b) to ~~obtain~~ calculate Si storage of main oil-palm parts. Si storage in the total above~~-~~ground biomass of an oil palm was calculated by adding up the amounts of Si stored in an oil-palm stem, in a palm crown composed of 40 mature palm fronds and in 12 – 14 fruit bunches, which is considered an average annual production of a mature oil palm (Corley and Tinker, 2016) (Tab. 2~~1~~c). Si storage in the above~~-~~ground oil-palm biomass of one~~1~~ hectare oil-palm plantation was calculated by multiplying the amount of Si stored in one mature oil palm by the average oil-palm planting density. All calculations were done for well-drained and riparian sites individually. The dry weights of oil-palm main parts obtained from literature only included data from mature oil palms (≥ 6 years) and were further distinguished ~~between well-drained and riparian sites~~according to WRB reference soil group. Fruit-bunch biomass ~~may~~ varied~~y~~ noticeably among oil palms, whereas the other main parts~~,~~ showed less variability in their dry biomass. Therefore, dry biomass ranges are presented only for fruit bunches.

Table 21a. Dry biomass estimates of main parts of mature oil palms in SE Asia and percentage relative contributions of oil-palm subparts to the biomass of the main parts

Water regime[a]	Main oil-palm part	Average bBiomass contributions of oil-palm subparts to main part [wt. %]	Dry biomass of main part [kg]	Oil-palm age [yr]	Reference Soil Group (WRB)[g]	Country
WD	Oil-palm stem	Stem (57), frond bases (43)	321[d]	12	Histosol[h]	Malaysia
WD	Oil-palm stem	Bare stem (100)	182[d]	12	Histosol[h]	Malaysia
WD	Frond no. 9	Leaflet (25), rachis (75)[b]	5[e]	6 - 14	Ferrasol	Malaysia
WD	Frond no. 17	Leaflet (25), rachis (75)[b]	5[e]	6 - 14	Ferrasol	Malaysia
WD	Senescing frond	Leaflet (25), rachis (75)[b]	5[e]	6 - 14	Ferrasol	Malaysia
WD	Palm crown	Leaflet (25), rachis (75)[b]	200	6 - 14	Ferrasol	Malaysia
WD	Fruit bunch	Stalk (33), pulp (33), kernel (33)[c]	5 - 20[f]	18 - 22	Acrisol	Indonesia
RI	Fruit bunch	Stalk (33), pulp (33), kernel (33)[c]	6 - 19[f]	11 - 21	Stagnosol	Indonesia

[a]WD = well-drained, RI = riparian
[b]this study, personal communication M. Kotowska
[c]averagepercentage share estimated to represent the mean of the three fruit-bunch components
[d]Lewis et al. (2020) / [e]Corley et al. (1971) / [f]data from this study
[g]WRB = IUSS Working Group WRB (2022): World Reference Base for Soil Resources, fourth edition
[h]stem biomass data of mature oil palms in SE Asia were only found for drained Histosols

Table 21b. Calculation of average Si storage in main oil-palm parts of mature oil palms in SE Asia, based on Si concentrations in the contained subparts, and the biomass that the subpart contributes to the main oil-palm part

Water regime[a]	Main oil-palm parts	Mean Si concentrations [wt. %] in the contained subparts[c]	Estimated average Si storage in main oil-palm parts [kg][de]
WD	Oil-palm stem	Stem (1.13)[b], frond bases (0.32)	2.51
WD	Oil-palm stem	Bare Stem (1.13)[b]	2.06
WD	Frond no. 9	Leaflet (1.06), rachis (0.29)	0.02
WD	Frond no. 17	Leaflet (1.74), rachis (0.29)	0.03
WD	Senescing frond	Leaflet (3.58), rachis (0.29)	0.06
WD	Palm crown	Leaflet (1.,74), rachis (0.29)	1.31
WD	Fruit bunch	Stalk (0.44), pulp (0.37), kernel (0.26)	0.02 – 0.07
RI	Oil-palm stem	Stem (1.13)[a], frond bases (0.31)	2.50
RI	Oil-palm stem	Bare stem (1.13)[a]	2.06
RI	Frond no. 9	Leaflet (1.08), rachis (0.29)	0.02
RI	Frond no. 17	Leaflet (1.34), rachis (0.29)	0.03
RI	Senescing frond	Leaflet (3.74), rachis (0.29)	0.06
RI	Palm crown	Leaflet (1.,34), rachis (0.29)	1.11
RI	Fruit bunch	Stalk (0.48), pulp (0.43), kernel (0.28)	0.02 – 0.07

[a]WD = well-drained, RI = riparian
[b]Pratiwi et al. (2018) determined the SiO_2 concentration in the oil-palm stem, which we converted to Si concentration (2.41 wt. % SiO_2 equaling 1.,13 wt. % Si)
[c]Total Si concentrations including error terms and number of replicates are shown in Table B1 in the appendix.
[de]calculated by multiplying the mean Si concentration of each oil-palm sub part by the biomass that the sub-part contributes to the main oil-palm part; data for fruit bunches mark the range that results from the highly variable fruit-bunch biomass

Table 2~~1~~c~~.~~ Si storage calculation in the above-ground oil-palm biomass in 1 hectare of oil-palm plantation

Water regime[a]	Main parts	Calculation assumptions	Si storage[d] [kg]
WD	One mature oil-palm tree	Stem, crown, 12 - 14 fruit bunches per year	4 - 5
WD	Mature oil-palm plantation (1 ha)	142 oil palms per hectare	572 - 682
WD	Annually pruned palm fronds (1 ha)	14 - 16 pruned fronds per palm, 142 oil palms per hectare[b]	111 - 126
WD	Fruit-bunch harvest in 2015 (1 ha)	15 - 20 Mg ha^{-1} fruit-bunch harvest[c]	54 - 72
WD	Fruit bunch harvest in 2018 (1 ha)	9 - 14 Mg ha^{-1} fruit-bunch harvest[b]	32 - 50
RI	One mature oil-palm tree	Stem, crown, 12 - 14 fruit bunches per year	4 - 5
RI	Mature oil-palm plantation (1 ha)	142 oil palms per hectare	551 - 660
RI	Annually pruned palm fronds (1 ha)	14 - 16 pruned fronds per palm, 142 oil palms per hectare[b]	115 - 131
RI	Fruit-bunch harvest in 2018 (1 ha)	9 - 11 Mg ha^{-1} fruit-bunch harvest[b]	32 - 40

[a]WD = well-drained, RI = riparian
[b]personal communication A. Tjoa
[c]Kotowska et al. (2015)
[d]data in the fourth column of the table mark the range of Si storage in the oil-palm parts listed in the second column, calculated based on the assumptions shown in the third column.

In addition to the amount of Si stored in oil palms, we also calculated Si return to soils through pruned palm fronds and Si losses through fruit-bunch harvest (Tab. 2~~1~~c). Our estimates of Si return to soils were based on 14 – 16 pruned palm fronds per palm each year, considering ~~due to~~ the average age of ~~these~~ the investigated oil palms (Woittiez et al., 2017, personal communication, A. Tjoa). Our Si loss-estimates ~~of Si losses~~ through fruit-bunch harvest were based on the harvests of two years in Jambi Province, i.e., the harvests of the years 2015 (well-drained) and 2018 (well-drained and riparian) (Kotowska et al., 2015, this study). We multiplied the average annual fruit-bunch harvest of these two years by the mean Si concentration of a fruit bunch to estimate ~~the~~ annual Si losses through fruit-bunch harvest. Again, these calculations were ~~made~~ done individually for well-drained and riparian sites.

2.5 Statistics

Statistical analyses were conducted on the grand means of three palm trees (n = 3) in four replicate plots at well drained and at riparian sites (n = 4 each). No senescing frond could be sampled at the riparian site HOr2, as ageing fronds were pruned ~~well before they died off~~early to maintain a high crop yield (personal communication, smallholder farmers). Statistical analyses were done on log-transformed data. Normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene test) were tested for all groups. We conducted a one-way analysis of variances (ANOVA) to test if the Si concentration of each oil-palm part differed significantly between the two water regimes. We conducted a Tukey-Kramer post-hoc test to examine, which oil-palm parts differed significantly in their Si concentrations. Statistical significance was assigned at $p \leq 0.05$ in all analyses. We used the open-source software R version 3.6.2 and R CRAN packages ggplot2 (Wickham 2016, https://ggplot2.tidyverse.org, last access 10 August 2022), car (Fox and Weisberg 2019, https://socialsciences.mcmaster.ca/jfox/Books/Companion/, last access 10 August 2022) and psych (Revelle 2019, https://CRAN.R-project.org/package=psych, last access 10 August 2022) to perform statistical analyses.

For ~~the~~ well-drained sites, we ~~fitted~~ fitted a trendline ~~of best fit~~ to test if Si accumulated with frond age. The trendline was fitted to the grand means (n = 4 plantations, n = 2 oil palms per plantation) of four mature frond leaflets (no. 9, no. 17, no. 22, and no. 25). The senescing frond was plotted as frond no. 39 although the exact frond no. was not determined in the field.

3 Results

3.1 Si and Ca concentrations in oil-palm parts

At well-drained sites, leaflets of all analysed palm fronds had a mean Si concentration of at least 1 wt. % Si, whereas ~~the~~ rachises, frond bases, fruit-bunch stalks, fruit pulp and kernels had mean Si concentrations below 0.5 wt. % Si (Fig. 2a). Mean Si concentrations in leaflets of frond no. 9 (1.06 ± 0.38 wt. % Si), leaflets of frond no. 17 (1.74 ± 0.47 wt. % Si) and leaflets of the senescing frond (3,58 ± 0.59 wt. % Si) were also significantly higher ($p \leq 0.05$) compared to those of the fruit-bunch stalk (0.44 ± 0.06 wt. % Si), frond base (0.32 ± 0.09 wt. % Si), rachis (0.29 ± 0.03 wt. % Si), fruit pulp (0.37 ± 0.07 wt. % Si) and kernel (0.26 ± 0.07 wt. % Si) (Fig. 2a, a~~A~~ppendix, Table B1). Mean Si concentrations in leaflets of the senescing palm frond were significantly higher ($p \leq 0.05$) than Si concentrations in leaflets of frond no. 17 and leaflets of frond no. 9, while mean Si concentrations did not differ significantly between the latter two. All oil-palm parts showed a Si/Ca weight ratio ≥~~≥~~ 1, except for the rachises, which had a Si/Ca weight ratio of 0.5 (a~~A~~ppendix, Table B1).

At riparian sites, mean Si concentrations followed a similar trend as at the well-drained sites (Fig. 2a, 2b). Again, leaflets of palm fronds had significantly higher Si concentrations ($p \leq 0.05$) in their tissue than ~~the~~ other oil-palm parts (Fig. 2b). Mean Si concentrations increased with age from 1.08 ± 0.44 wt. % Si in leaflets of palm frond no. 9 to 3.74 ± 1.13 wt. % Si in leaflets of the senescing palm frond (Fig. 2, a~~A~~ppendix, Table B1). Si concentrations in leaflets of the senescing palm fronds were significantly higher ($p \leq 0.05$) than those in leaflets of palm frond no. 9 and palm frond no. 17 (Fig. 2b). In contrast, mean Si concentrations in the rachises, frond bases, fruit bunch stalks, fruit pulp and kernels were in a similar range of around 0.3 to 0.5 wt. % Si (Fig. 2b). R~~The r~~achises had the smallest Si/Ca ratio of 0.7, whereas leaflets of the senescing palm frond had the largest Si/Ca ratio of 4.3 (a~~A~~ppendix, Table B1). When comparing Si concentrations of the same oil-palm part (e.g., rachis) between ~~the~~ well-drained and the riparian sites (HO and HOr), Si concentrations were similar.~~,~~ N~~and n~~o significant differences were detected (a~~A~~ppendix, Table B1).

At well-drained sites, we additionally assessed how Si accumulated with leaf age in more detail. Mean Si concentrations in leaflets of four mature palm fronds increased linearly ($R^2 = 0.98$) with palm-frond age (Fig. 3).

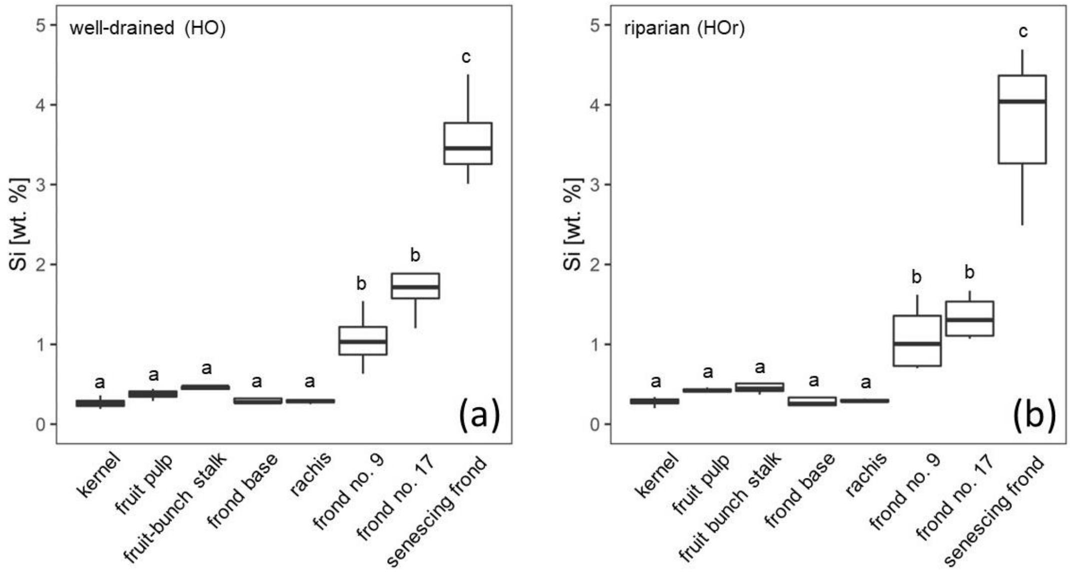

Fig. 2 Si concentrations in oil-palm subparts at well-drained (a) and riparian sites (b). Lower case letters indicate significant differences ($p \leq 0.05$) between oil-palm subparts within the same water regime. n = 4 for each plant part, except for the senescing frond which is n = 3 at riparian sites.

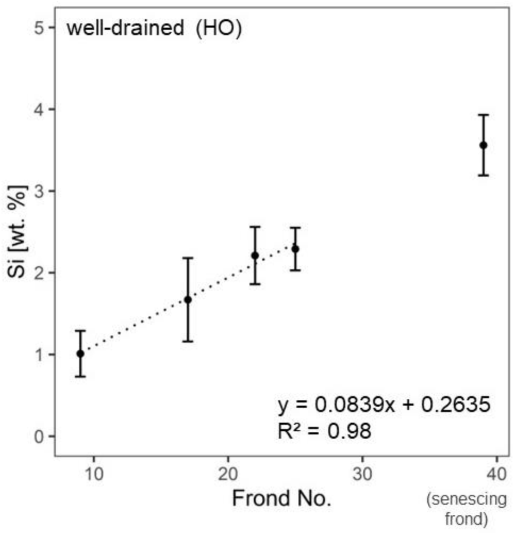

Fig. 3 Si concentrations in leaflets of five mature oil-palm fronds (no. 9, 17, 22, 25, senescing palm frond) from well-drained areas.

3.2 Si storage in the above~~-~~ground biomass of oil palms, Si return to soils through decomposing pruned palm fronds, and Si losses through harvest on smallholder oil-palm plantations

Calculating Si storage in the aboveground biomass of oil palms required biomass data for all plant parts. As it was not permitted to cut-down oil palms to determine the stem and frond-base biomass per palm tree, we used mean biomass estimates of mature oil palms in SE Asia from literature (Tab.~~le~~ 2~~1~~a). ~~summarizes mean biomass estimates of the analysed oil-palm parts from mature oil palms in SE Asia.~~ Lewis et al. (2020) calculated the average biomass of a bare oil-palm stem (~182 kg) and a stem including palm-frond bases (~321 kg). This data suggests that palm-frond bases add another ~40 wt. % of biomass to an oil-palm stem. Corley et al. (1971) estimated a mature oil-palm frond to weigh ~5 kg. Based on these literature data and our own observations, we estimated a palm crown composed of 40 fronds to weigh roughly ~200 kg, which is in the same range as a bare oil-palm stem. In comparison, a single fruit bunch ~~can~~ weighed between 5 kg and 20 kg (a~~A~~ppendix, Table B2).

Si storage in the analysed oil-palm parts was similar at well-drained and riparian sites (Tab. 2~~1~~b). Among all analysed parts, the oil-palm stem contributed most to the estimated Si storage of one palm tree, amounting to 2.0 – 2.5 kg Si. Thereby, palm-frond bases that are attached to the palm stem up to an age of at least 12 years contributed about 20 wt. % ~~of this amount of~~ Si ~~was contributed by palm-frond bases that are attached to the palm stem up to an age of at least 12 years~~(Corley and Tinker, 2016). Compared to the stem, an oil-palm crown~~,~~ composed of 40 palm fronds~~,~~ stored roughly half the amount of Si, about ~1.2 kg. The 12 – 14 fruit bunches produced by a palm tree each year stored 0.24 – 0.98 kg Si (0.02 – 0.07 kg Si per fruit bunch). In oil-palm fronds, Si storage increased with palm-frond age from 0.02 kg Si in frond no. 9 to 0.06 kg Si in a senescing frond.

According to our calculations, smallholder plantations at well-drained and riparian sites showed similar Si storage in the total above~~-~~ground biomass of oil palms, Si return through decomposing palm fronds, and Si losses through fruit-bunch harvest (Tab. 2~~1~~c). ~~At well-drained sites, T~~The above~~-~~ground biomass of a mature oil palm was estimated to store about 4 – 5 kg ~~of~~ Si. Consequently, oil palms in a one~~1~~ hectare ~~of~~ smallholder oil-palm plantation stored at least 550 kg ~~of~~ Si in their above~~-~~ground biomass. Annual Si return to the topsoil via pruned palm fronds ~~was estimated to~~comprised at least 110 kg Si ha^{-1}~~per hectare~~. About 50 – 70 kg Si ~~per hectare~~ha^{-1} were lost by annual fruit bunch harvest in 2015, about 30 – 50 kg Si ~~per hectare~~ha^{-1} in 2018.

4 Discussion

4.1 Si distribution and accumulation in various oil-palm parts

L~~In all palm l~~eaflets of all investigated palm frond had~~,~~ ~~we found~~ mean Si concentrations of ≥~~≥~~ 1 wt. % and a Si/Ca mass ratio ~~of~~ > 1. ~~In addition~~Furthermore, the Si concentration increased with leaf age. Thus, our results reconfirmed the classification of oil palms being Si hyper-accumulators (Ma and Takahashi, 2002). ~~According to Ma and Takahashi (2002), Si concentration > 1 wt. %, a Si/Ca mass ratio > 1, and an increase of mean Si concentration with frond age suffices for a plant to be classified as a Si accumulator. Our results correspond well with earlier findings of Munevar and Romero (2015). However, several authors proposed to also consider uptake mechanisms as a criterion for Si-accumulating plants, especially when addressing matters related to nutrient availability and a potential need for Si fertilizer application: only Si accumulators with an active Si-uptake and Si-transport mechanism (Guntzer et al., 2012; Liang et al., 2015) are likely to deplete easily soluble to strongly bound Si pools in soils (Liang et al., 2015), but not those with passive Si uptake. Si accumulators with an active uptake~~

and transport mechanism include rice, barley, and wheat. These plants have specific transporter genes (Lsi1, Lsi2 and Lsi6) that translocate Si between the roots, transpiration stream and final deposition sites (Liang et al., 2015). These specific transporter genes were discovered in grains and straw residues of the above-mentioned crops by gene encoding, but such analyses have not yet been conducted for oil palms. Alternatively, Si uptake by oil-palms roots could also resemble that of heavy-metal uptake of hyperaccumulating plants. These plants accumulate heavy metals in their rhizosphere (Balafrej et al., 2020; Rascio and Navari-Izzo, 2011) before relocating and precipitating them in high concentrations in leaf tissue. Whether a similar mechanism also applies to Si uptake by oil-palm roots has not been investigated yet.

At both well-drained and riparian sites, our principal observation was that mean Si concentrations in leaflets of oil-palm fronds ($\geq \gtrsim$ 1 %) were significantly higher compared to all other above-ground oil-palm parts ($\leq$ 0.8 %) (Fig. 2). These observations correspond well to findings of Munevar and Romero (2015), and Carey and Fulweiler (2016), who reported higher Si concentrations in leaf tissue compared to other plant parts in Si hyper-accumulators, as well.

In plants, Si remains dissolved in the transpiration stream (Carey and Fulweiler, 2012; Epstein, 1994) until it reaches epidermal cell walls, the cell lumen, and intercellular spaces in the leaves (Epstein, 1994). This may be explained by High Si concentrations in leaflets are the results of Si preferentially precipitating at final transpiration sites, i.e., in the leaflets(Carey and Fulweiler, 2012). In contrast to the leaflets, significantly lower mean Si concentrations in palm-frond bases and rachises could imply that these plant parts are related to the transpiration stream rather than to transpiration and associated Si precipitation. Instead, This may explain the significantly lower mean Si concentrations in their tissues. Once precipitated in leaf tissue, Si remains immobile and accumulates over time (Epstein, 1994). Since the process of transpiration and associated Si precipitation in leaflets seem continues over the lifetime of an oil-palm frond, it results in a continuous increase of the mean Si concentration in the leaflets with palm-frond age that and can be described well by a linear equation (Fig. 3). It is assumed that Si first accumulates in lower (abaxial) epidermal cells and with time in upper (adaxial) epidermal cells (Epstein, 1994).

Lower mean Si concentrations in the various fruit-bunch parts (stalk, fruit pulp and kernel) suggest that Si is present in fibres, but barely in the hard shell and oily endosperm of the kernel (Omar et al., 2014). According to Omar et al. (2014)In the fruit-bunch stalk, Si is either partly embedded within the surface, or precipitates directly on the surface of fruit-bunch fibres., but(i.e., the fruit-bunch stalk) . However, in fruit-bunch stalk, Si does not precipitate in cell walls (Omar et al., 2014). Despite low mean Si concentrations in various fruit-bunch parts, a considerable amount of Si is exported through harvest each year. In 2015, the annual fruit-bunch harvest amounted to about 15 – 20 Mg ha^{-1} dry biomass on well-drained plantations within our study area (Kotowska et al., 2015). This corresponded to an export of 54 – 72 kg ha^{-1} Si from the system (56 – 74 kg ha^{-1} Si if 8% underestimation by Na_2CO_3 extraction from fruit-bunch stalks is considered as reported in chapter 2.3.1). In 2018, the yield was lower in plantations of both well-drained and riparian areas, with 9 – 14 Mg ha^{-1} dry biomass, corresponding to an Si export of 32 – 50 kg ha^{-1}(33 – 52 kg ha^{-1} if 8% underestimation is considered). Thus, Si losses through fruit-bunch harvest were similar for both well-drained and riparian areas..

According to Corley and Tinker (2016), the central part of the stem of the oil palm includes some Si-containing tissue in its central part, as well (Fig. 1b). Si precipitation in the stem may take place along the vascular system or in cell walls. Epstein (1994) assumed that stabilizing the stem through silicifying cells can be a beneficial strategy of plants~~,~~ as it requires less energy than stabilizing the stem by ~~other materials such as~~ cellulose.

Overall, our results suggest that among all oil-palm parts, palm leaflets accumulate Si most effectively in their tissue. Thus, the management of palm fronds plays a key role in driving and maintaining Si cycling on oil-palm plantations. However, our study also shows that Si precipitates in all above-ground oil-palm subparts. Therefore, specific Si concentrations of all oil-palm parts need to be analysed individually and~~, and further need to be~~ upscaled to palm tree and plantation level. This allows to evaluate potential impacts of oil-palm cultivation and management practices on Si cycling.

4.2 Identified Si storage, cycling, and losses on smallholder oil-palm plantations, and favourable management practices

4.2.1 Comparison of plantations in well-drained and riparian areas

At well-drained and riparian sites, smallholder oil-palm plantations showed similar Si storage in the total above-ground biomass of oil palms, Si return to soils through decomposing oil-palm fronds, and Si losses through fruit-bunch harvest (Tab. 2c). We assume that t~~T~~his was due to similar Si concentrations in the respective oil-palm parts in both water regimes~~,~~ and because the same biomass data was used to calculate Si storage capacities for all sites (Tab. 2~~1~~a). The number of studies providing oil-palm biomass data is still scarce to have been able to distinguish between riparian and well-drained soils. Therefore, our hypotheses were only partially verified: oil palms store noticeable amounts of Si in their biomass. However, an additional influx of dissolved silicic acid through flooding, capillary rise of groundwater and lateral water fluxes (interflow) from higher-lying areas did not increase Si storage in oil-palm plantations of riparian areas.

4.2.2 Favourable management practices using palm fronds and fruit-bunch parts

In our study area, one hectare of smallholder oil-palm plantation stored about 551 – 682 kg Si in the total aboveground biomass. Pruned palm fronds returned ~111 – 131 kg Si each year to the topsoils (Fig. 4). Annual Si losses through fruit-bunch harvest amounted to 32 – 72 kg ha^{-1} yr^{-1} (33 – 74 kg ha^{-1} yr^{-1} if 8% underestimation by Na_2CO_3 is considered) which corresponds to around 6 – 10% of the amount of Si stored in the total aboveground biomass. Although much Si is recycled in the system by the practice of frond-pile stacking, it could still be optimized, e.g., by changing the positions of frond piles every 5 – 10 years. Such practices would lead to a more evenly distributed Si return to topsoils across plantations.

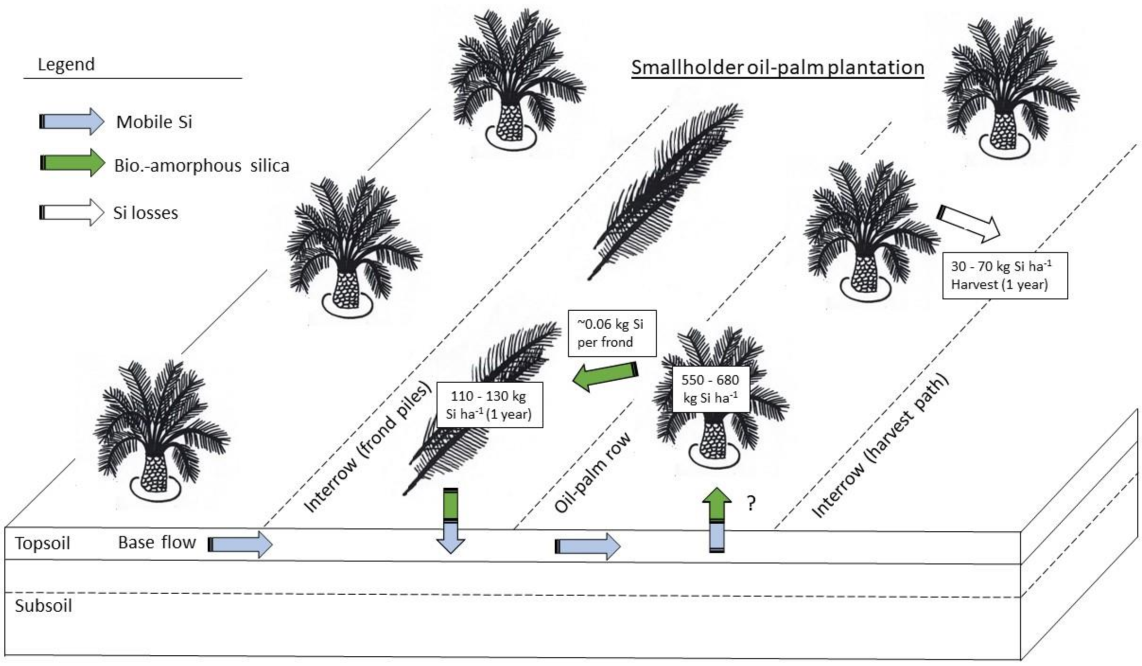

Fig. 4 Si storage in the aboveground biomass of oil palms, Si return to soils through decomposing pruned palm fronds, and Si losses through harvest on smallholder oil-palm plantations in Jambi Province, Sumatra.

The relevance of Si losses by harvest has been previously addressed by Puppe et al. (2021), Guntzer et al. (2012b) and Vandevenne et al. (2012). In our study, Si storage in fruit bunches was localized mainly in the fruit-bunch stalk and fruit pulp (section 4.1). Like oil palms, many Si hyper-accumulators store less Si in their grains than in the harvest residues (Carey and Fulweiler, 2016; Hughes et al., 2020; Vandevenne et al., 2012): in wheat (*Triticum aestivum*), oat (*Avena sativa*) and barley (*Hordeum vulgare*) straw, the mean Si concentration was higher than in the respective cereal grain (Vandevenne et al. (2012). Hughes et al. (2020) found rice grains (*Oryza sativa*) under different rice-residue management practices to accumulate 59 ± 43 kg Si ha^{-1} yr^{-1}, but rice straw to accumulate 82 ± 25 kg Si ha^{-1} yr^{-1}. Carey and Fulweiler (2016) as well as Guntzer et al. (2012) made similar observations and concluded that non-edible plant parts (e.g., straw) could serve well as an organic fertilizer. These observations highlight the importance of managing harvest residues.

Indeed, fruit-bunch harvest may alter Si cycling with time, although a significant impact may only be seen on a longer term than covered by this study (Clymans et al., 2011; Guntzer et al., 2012). Therefore, we recommend reducing Si losses through harvest by returning the empty fruit bunches (the residues not used to produce palm oil) to the palm circle on smallholder plantations. In this way, empty fruit bunches may serve as organic fertilizer and may increase amounts of bioavailable Si in the rooting area of the oil palm. This is already common practice on state-owned oil-palm plantations. However, it remains low priority for smallholder farmers because of the logistical effort and costs involved in the transport of empty fruit bunches back to oil-palm plantations (Woittiez et al., 2018; Euler et al., 2016a).

4.2.2 Favourable management practices using stem residues

A single mature oil palm stored 4 – 5 kg Si in its total above-ground biomass (Tab. 1c). Thereby, the oil-palm stem stored twice the amount of Si (2.0 – 2.5 kg Si) in its biomass (182 – 321 kg) compared to the palm crown that stored 1.1 – 1.3 kg Si in its biomass (200 kg) (Tab. 1b). The average annual fruit-bunch production per palm tree corresponded to 0.24 – 0.98 kg Si in the fruit-bunch biomass (60 – 280 kg; based on 12 – 14 fruit bunches and a biomass of 5 – 20 kg per fruit bunch) (Tab. 1c). Si concentrations in the stem (Tab. 21b) may seem negligiblelow.; Yyet, multiplying its the Si concentration by the large stem biomass (Aholoukpè et al., 2018) (accounting for 50 % of the entire oil-palm biomass; Aholoukpè et al., 2018) showeds that the stem provides the largest Si pool of the oil palm's above-ground biomass. In contrast, palm leaflets showed the highest Si concentrations (Tab. 21b) but contributed only 25 wt. % to the biomass of a palm frond. This lead s to smaller total Si storage in the crown compared to the stem of a palm tree. Both oil-palm parts are highly relevant for Si cycling in the system. WThus, we strongly recommend keeping both the stem and the palm-frond residues on the plantation, especially when an oil-palm plantation is cleared for replanting. Oil palms could benefit from Si fertilization like other Si hyper-accumulators (Klotzbücher et al., 2018; Datnoff et al., 1997; Li and Delvaux, 2019).

Oil-palm plantations are usually cultivated for about 25 years (Corley and Tinker, 2016). Thereafter,after which the oil-palm stem is considered a waste product (Onoja et al., 2019; Awalludin et al., 2015). It used to be common practice to burn the stem, as the ash was regarded to sustain soil fertility (Selamat et al., 2019) by releasing Si and other nutrients into topsoil (Selamat et al., 2019; von der Lühe et al., 2020). Yet, these nutrients, including Si, are released from the ash in such high amounts and so quickly rapidly that they are highly susceptible to leaching. It is likely that Mmany nutrients are could be lost from the system before a new generation of oil palms can take them up. Thus, despite the short-term fertilizing effect of the ash, this process may enhance nutrient and Si depletion for the long term (von der Lühe et al., 2020). Nowadays, replanting follows a zero-burning policy (Corley and Tinker, 2016) to reduce greenhouse gas emissions and, air pollution. Furthermore,, and tothis policy shall prevent fires from getting out of control and which could impacting natural vegetation. Without burning, most stem biomass remains on the plantations, as it has no monetary value for industrial or agricultural applications (Awalludin et al., 2015; Onoja et al., 2019). Currently, oil-palm stems are chipped and then distributed as an organic fertilizer at the end of a 25-year plantation cycle (Corley and Tinker, 2016). It has been suggested to provide governmental support to implement this practice on smallholder plantations, as well (Woittiez et al., 2018). However, this practice has not yet been widely used as many oil-palm plantations in Jambi Province (including those in our study area) are only on the verge of being replanted in the next decade.

In view of the large area (~16 million hectares) under oil-palm cultivation in Indonesia (Gaveau et al., 2022), governments are interested in finding economically more lucrative applications for oil-palm residues (Awalludin et al., 2015; Chang, 2014; Rubinsin et al., 2020; Santi et al., 2019), including stems (Awalludin et al., 2015) that could boost the economy and benefit smallholder farmers. As a result, most research focusses on economically beneficial applications, e.g., in the renewable energy sector such as for fuel and gas production, but also for production of composites and fertilizers (Onoja et al., 2019). Currently, oil-palm stems, are chipped, and then distributed as an organic fertilizer at the end of a 25-year plantation cycle(Corley and Tinker, 2016). A clear advantage of the current practice, i.e., spreading chipped stem parts across the plantation as an organic fertilizer, is that it supports the system's internal nutrient and Si cycling. This reduces the need to buy industrial fertilizers and avoids any costs and carbon dioxide emissions related to the transport of the stems. Selling the biomass waste for industrial purposes, the production of building materials (e.g., gypsum composites and wood fibre alternatives) (Selamat et al., 2019; Pratiwi et al., 2018; Dungani et al., 2013) or for paper production (Pratiwi et al., 2018) would mean that farmers would have to compensate for the nutrient export from their plantations by buying more industrial fertilizers. In addition, both the transport of the palm stems from the plantations and the transport of fertilizers to the plantations would involve costs and carbon dioxide emissions. It has been suggested to provide governmental support to implement this practice on smallholder plantations, as well (Woittiez et al., 2018). However, this practice has not yet been widely used, as many oil-palm plantations in Jambi Province (including those in our study area) are only on the verge of being replanted in the next decade.

In view of the large area under oil-palm cultivation of ~16 million hectares in Indonesia(Gaveau et al., 2022), governments are interested in finding economically more lucrative applications for oil-palm residues (Awalludin et al., 2015; Chang, 2014; Rubinsin et al., 2020; Santi et al., 2019), including stems (Awalludin et al., 2015) that could boost the economy and benefit smallholder farmers. As a result, most research focusses on economically beneficial applications, e.g., in the renewable energy sector such as for fuel and gas production, but also for production of composites and fertilizers (Onoja et al., 2019). A clear advantage of spreading the chipped stem parts across the plantation as an organic fertilizer is that this practice supports the system's internal nutrient and Si cycling. This reduces the need to buy industrial fertilizers and avoids any costs and carbon dioxide emissions related to the transport of the stems. Selling the biomass waste for industrial purposes and the production of building materials (e.g., gypsum composites and wood fibre alternatives) (Selamat et al., 2019; Pratiwi et al., 2018; Dungani et al., 2013)or for paper production (Pratiwi et al., 2018)would mean that farmers would have to compensate for the nutrient export from their plantations by buying more industrial fertilizers. In addition, both the transport of the palm stems from the plantations and the transport of fertilizers to the plantations would involve costs and carbon dioxide emissions.

Within our study area, one hectare of smallholder oil-palm plantation was estimated to store about 0.5 – 0.7 Mg Si, and pruned palm fronds to return ~110 – 130 kg Si each year to the topsoils (Fig. 4). Amounts of Si stored in the above-ground biomass of oil palms, and those returned to soils through decomposing pruned palm fronds were larger than Si losses through fruit-bunch harvest. These data suggest that Si cycling is maintained in this system. Nevertheless, the practice of frond-pile stacking could be optimized, e.g., by stacking palm fronds not always in the same interrows over the entire plantation cycle of 25 years but stacking them in interrows previously serving as harvesting paths after about 5 – 10 years. Such practice would lead to a more evenly distributed Si return to the topsoils across the plantations. In addition, management of fruit bunches could be improved. Si storage in fruit bunches was localized mainly in the fruit-bunch stalk and fruit pulp (section 4.1), which means that this Si is lost from the system when the fruit bunches are harvested. Though this loss may seem negligible initially, the annual fruit-bunch harvest in 2015 and 2018 in our study area involved considerable Si losses (32 – 72 kg ha^{-1} yr^{-1}) (Fig. 4). In comparison, Vandevenne (2012) found maize grains (*Zea mays*) to incorporate 4 – 5 kg Si ha^{-1} yr^{-1}. Hughes et al. (2020) found rice grains (*Oryza sativa*) under different rice-residue management practices to accumulate 59 ± 43 kg of Si ha^{-1} yr^{-1}. Vandevenne et al. (2012) recommended not to neglect these Si losses through harvest. Indeed, fruit-bunch harvest may alter Si cycling over time, although a significant impact may only be seen on a longer term than covered by this study. Therefore, we recommend reducing Si losses through harvest by returning the empty fruit bunches to the palm circle on smallholder plantations. In this way, empty fruit bunches may serve as organic fertilizer and may increase Si availability in the rooting area of the oil palm. This is already common practice on state-owned oil-palm plantations, but it remains low priority for smallholder farmers, because of the logistical effort and costs involved in the transport of the empty fruit bunches back to the oil-palm plantations (Woittiez et al., 2018).

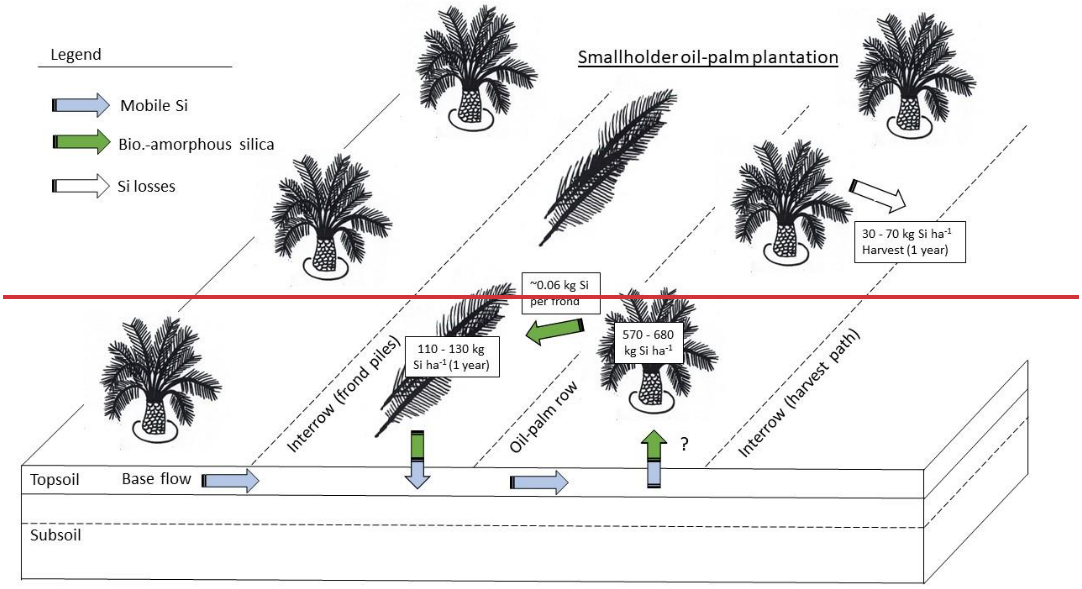

Fig. 4 Si storage in the above-ground biomass of oil palms, Si return to soils through decomposing pruned palm fronds, and Si losses through harvest on smallholder oil-palm plantations in Jambi Province, Sumatra.

5 Conclusions

In this study, we assessed the amounts of Si involved in internal Si cycling in the oil-palm system as well as the amounts of Si leaving the system through fruit-bunch harvest. Our study reconfirmed previous assumptions in that oil palms can ~~We conclude that the oil palm fulfils several criteria to~~ be considered ~~a~~ Si hyper-accumulators (mean Si concentration >~~≥~~ 1 wt. % in leaflets, Si/Ca mass ratio >~~≥~~ 1).~~;~~ M~~m~~ean Si concentrations increase~~d~~ds with leaf age~~)~~. A senescing frond stored three~~3~~-times the amount of Si in its leaf tissue compared to a ~~barely~~ mature palm frond. ~~Yet an oil-palm stem had the highest~~Total Si storage ~~potential due to its high~~in the biomass ~~when regarding Si storage~~ of ~~an~~ mature oil palms amounted to 551 – 682 kg ha^{-1}. Oil-palm stems stored the greatest amounts of Si per hectare due to their large biomass. Therefore, keeping oil-palm stems (including frond bases) in the system could be an effective measure of maintaining balanced Si levels on the long-term, i.e., over several oil-palm generations. On the short-term, i.e., within one oil-palm generation, pruning and stacking palm fronds in frond piles turned out to be an effective management practice. This practice returned 111 – 131 kg Si per hectare and year to soils. Nevertheless, we found that fruit-bunch harvest involved a considerable annual Si export of 32 – 72 kg ha^{-1} from the system. Consequently, fertilization may be needed after several oil-palm generations. We recommend the following management measures that enhance Si cycling in the system: (1) ensuring a spatially more even Si return from decomposing palm fronds to soils, e.g., by changing the position of frond-piles every 5 – 10 years (2) returning empty fruit bunches to the palm circle to serve as organic fertilizer; (3) leaving all oil-palm residues on the plantation after a plantation cycle of 25 years, especially oil-palm stems (chopped and evenly distributed across the plantation) although the use of these residues for industrial purposes may be financially attractive to plantation owners.

~~and an oil-palm plantation. For oil palms, Si was not a limiting factor after a 25-year-cultivation period yet. In fact, Si availability could suffice for a second generation of oil-palm plantations. However, as Si remains immobile in leaf tissue, i.e., there being no Si transfer from old palm parts to younger parts, and Si losses through fruit-bunch harvest continue, Si depletion in tropical soils may become an issue in the future. If this arises, fertilization may be needed, irrespectively of higher Si concentrations in mature and senescing fronds. We therefore recommend following management measures that enhance Si cycling in this system: (1) by returning empty fruit bunches to the palm circle to serve as organic fertilizer; (2) by leaving oil-palm residues on the plantation after a plantation cycle of 25 years, especially the oil-palm stem (chopped and evenly distributed across the plantation) although the use of these residues for industrial purposes may be financially attractive to plantation owners; (3) by optimizing frond-pile stacking, for instance, by moving frond-pile locations every 5 – 10 years. This would also ensure that Si is returned to the topsoil evenly across the plantations.~~

6 Appendices

Table A1 Sampling of oil-palm parts, fieldwork 2019

		**Palm fronds:** Oil palms and a detailed view of an oil-palm crown showing palm fronds of different age: mature palm fronds and senescing fronds.
		**Fruit bunches:** Oil-palm crown with ripe fruit bunches.
		**Fruit bunch:** A harvesting tool *Egreg* is used to cut off senescing fronds and ripe fruit bunches. Photo ~~credit~~: B. Greenshields

Table A1 continued

		**Frond bases:** Frond bases were cut off oil-palm stems at ~1.5 m height.
		**Oil-palm parts:** Ripe fruit bunch showing single fruit in fibrous casts. The fruit bunch is attached to the oil-palm stem by its fibrous stalk. Single leaflets of frond n~~N~~o. 9, 17 and a senescing frond (left to right) next to a piece of the rachis.
		**Oil-palm parts:** Sampled oil-palm parts were already cut and chopped in the field. Fruit was cut off the fruit bunch and left as such. Photo ~~credit~~: B. Greenshields

Table B1 Total Si and Ca concentrations in oil-palm parts and statistical analyses

Oil-palm part	Water regime[b]	N	Total Si [%] $\bar{x}$		σ	Ca [%] $\bar{x}$		σ	Si/Ca ratio	Shapiro-Wilk p-value (ND)	Levene p-value (VAR)
Frond no. 9	WD	4	1.06	±	0.38	0.50	±	0.12	2.1	0.95	
Frond no. 17	WD	4	1.74	±	0.47	0.63	±	0.11	2.8	0.72	
Senescing frond	WD	4	3.58	±	0.59	0.95	±	***0.10***	3.8	0.65	
Rachis	WD	4	0.29	±	0.03	0.54	±	0.12	0.5	0.69	0.06 '.'
Frond base	WD	4	0.32	±	0.09	0.24	±	0.05	1.3	***0.02***[c]	
Fruit-buch stalk	WD	4	0.44	±	0.06	0.40	±	0.12	1.1	***0.01***	
Fruit pulp	WD	4	0.37	±	0.07	0.15	±	0.05	2.4	0.91	
Kernel	WD	4	0.26	±	0.07	0.07	±	0.02	3.9	0.84	
Frond no. 9	RI	4	1.08	±	0.44	0.39	±	0.11	2.7	0.35	
Frond no. 17	RI	4	1.34	±	0.29	0.49	±	0.10	2.7	0.38	
Senescing frond[a]	RI	3	3.74	±	1.13	0.88	±	0.06	4.3	0.56	
Rachis[a]	RI	3	0.29	±	0.03	0.44	±	0.10	0.7	0.78	***0.02 '*'***
Frond base	RI	4	0.31	±	0.14	0.21	±	0.04	1.5	***0.03***	
Fruit-buch stalk	RI	4	0.48	±	0.12	0.35	±	0.13	1.4	0.34	
Fruit pulp	RI	4	0.43	±	0.03	0.15	±	0.08	2.9	0.69	
Kernel	RI	4	0.28	±	0.06	0.10	±	0.03	2.9	0.73	

[a] n=3 as no senescing fronds were left handing on palm trees (differing management practice on HOr2)
Statistics was done with the non-parametric Kruskal-Wallice test and Whitney-Mann-U test.
[b]WD = well-drained, RI = riparian
[c]Italic-bold = not asserted

Table B2 Morphological characteristics of oil palms taken for sampling and Si accumulation in fruit bunches.

Water regime[a]	Plot	Oil palm [#]	Stem [m]	Senescing fronds [#]	Fruit colour	FB[a] [#]	FFB [kg]	dry FB[b] [kg]	Si in dry FB [g]
WD	HO1	1	7	2	dark-red	≥1	17.6	9.3	33
WD	HO1	2	7	1	dark-red	2	15.6	8.2	30
WD	HO1	3	6	4	dark-red	≥1	18.7	9.9	36
WD	HO2	1	7 -~~to~~ 8	5	orange-red	1	8.9	4.7	17
WD	HO2	2	7 -~~to~~ 8	5	orange	1	16.7	8.8	32
WD	HO2	3	8	7	orange-red	≥1	13.2	6.9	25
WD	HO3	1	7	1	dark-red	≥1	19.0	10.0	36
WD	HO3	2	7	4	dark-red	≥1	13.0	6.8	25
WD	HO3	3	8	4	dark-red	6	36.8	19.4	70
WD	HO4	1	5	8	dark-red	4	13.0	6.9	25
WD	HO4	2	5	8	red	2	16.7	8.8	32
WD	HO4	3	6	9	dark-red	3	16.0	8.4	30
RI	HOr1	1	5	1	dark-red	4	12.6	6.6	27
RI	HOr1	2	6	4	dark-red	3	17.6	9.3	37
RI	HOr1	3	5	6	dark-red	5	16.7	8.8	35
RI	HOr2	1	4	0	dark-red	3	13.2	7.0	28
RI	HOr2	2	4	0	dark-red	3	16.7	8.8	35
RI	HOr2	3	4	0	dark-red	1	19.0	10.0	40
RI	HOr3	1	6	1	dark-red	≥1	24.0	12.6	51
RI	HOr3	2	6	1	dark-red	≥1	36.2	19.1	76
RI	HOr3	3	5	1 (green)	dark-red	≥1	19.2	10.1	40
RI	HOr4	1	5	from frond pile	dark-red	1	16.4	8.6	35
RI	HOr4	2	4	from frond pile	dark-red	1	18.9	10.0	40
RI	HOr4	3	5	2	dark-red	≥1	12.0	6.3	25

[a]WD and RI = well-drained and riparian areas; FB and FFB = Fruit bunch and fresh fruit bunch.
[b]Dry FB weight calculated after Corley et al. (1971). Si concentration in dry FB calculated by multiplying dry FB weight by mean Si concentration of fruit bunch components (stalk, fruit, kernel).

7 Data availability

Data are available upon request to the authors.

8 Supplement

Data is provided in the appendix of the manuscript.

9 Author's contribution

BvL and DS designed the study of the manuscript with input from HH and AT. BG conducted plant sampling with input from BvL and FB. MK and FB provided botanical and harvest data. FS conducted laboratory analysis with input from BvL and BG. FS and BG evaluated the data with input from BvL, HH, MK, FB, and DS. BG wrote the first draft. All authors (BG, BvL, FS, HH, AT, MK, FB, and DS) contributed to generating and reviewing the subsequent versions of the paper.

10 Competing interests

The authors declare that they have no conflict of interests.

11 Acknowledgements

We thank the German Research Foundation DFG for funding this project (DFG project no. 391702217). The project was associated to the Collaborative Research Center 990 "Environmental and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems" (CRC 990, DFG project no. 192626868). We also thank the Ministry of Education, Technology and Higher Education (RISTEKDIKTI) for granting a research permission in Indonesia and the CRC 990 oil-palm smallholder partners. Plant sampling was conducted using the research permit 187/ E5/E5.4/SIP/2019. Special thanks go to our Indonesian counterparts, the CRC-990 office members, our fieldwork assistants Nando and Toni in Jambi and our student assistant Kerstin in Göttingen. We would also like to thank the laboratory staff from the Institute of Geography, University of Göttingen, Jürgen Grotheer, Anja Södje and Petra Voigt, for their support.

12 Financial support

This project was funded by the German Research Foundation DFG (DFG project no. 391702217).

13 References

Aholoukpè, H. N. S., Dubos, B., Deleporte, P., Flori, A., Amadji, L. G., Chotte, J. L., and Blavet, D.: Allometric equations for estimating oil palm stem biomass in the ecological context of Benin, West Africa, Trees, 32, 1669–1680, https://doi.org/10.1007/s00468-018-1742-8, 2018.

Albakri, Z. M., Saufi, M., Kassim, M., Abdullah, A. F., and Harith, H. H.: SCIENCE & TECHNOLOGY Analysis of Oil Palm Leaf Phyllotaxis towards Development of Models to Determine the Fresh Fruit Bunch (FFB) Maturity Stages, Yield and Site-Specific Harvesting, Pertanika J. Sci. & Technol, 27, 659–672, 2019.

Alexandre, A., Meunier, J.-D., Colin, F., and Koud, J.-M.: Plant impact on the biogeochemical cycle of silicon and related weathering processes, Geochim Cosmochim Acta, 61, 677–682, https://doi.org/10.1016/S0016-7037(97)00001-X, 1997.

Allen, K., Corre, M. D., Kurniawan, S., Utami, S. R., and Veldkamp, E.: Spatial variability surpasses land-use change effects on soil biochemical properties of converted lowland landscapes in Sumatra, Indonesia, Geoderma, 284, 42–50, https://doi.org/10.1016/j.geoderma.2016.08.010, 2016.

Amirruddin, A. D., Muharam, F. M., and Mazlan, N.: Assessing leaf scale measurement for nitrogen content of oil palm: Performance of discriminant analysis and support vector machine classifiers, Int J Remote Sens, 38, 7260–7280, https://doi.org/10.1080/01431161.2017.1372862, 2017.

Awalludin, M. F., Sulaiman, O., Hashim, R., and Nadhari, W. N. A. W.: An overview of the oil palm industry in Malaysia and its waste utilization through thermochemical conversion, specifically via liquefaction, Renewable and Sustainable Energy Reviews, 50, 1469–1484, https://doi.org/10.1016/j.rser.2015.05.085, 2015.

Carey, J.: Soil age alters the global silicon cycle, Science (1979), 369, 1161–1162, https://doi.org/10.1126/science.abd9425, 2020.

Carey, J. C. and Fulweiler, R. W.: The Terrestrial Silica Pump, PLoS One, 7, 4, https://doi.org/10.1371/journal.pone.0052932, 2012.

Carey, J. C. and Fulweiler, R. W.: Human appropriation of biogenic silicon – the increasing role of agriculture, Funct Ecol, 30, 1331–1339, https://doi.org/10.1111/1365-2435.12544, 2016.

Chang, S. H.: An overview of empty fruit bunch from oil palm as feedstock for bio-oil production, Biomass Bioenergy, 62, 174–181, https://doi.org/10.1016/j.biombioe.2014.01.002, 2014.

Clough, Y., Krishna, V. v., Corre, M. D., Darras, K., Denmead, L. H., Meijide, A., Moser, S., Musshoff, O., Steinebach, S., Veldkamp, E., Allen, K., Barnes, A. D., Breidenbach, N., Brose, U., Buchori, D., Daniel, R., Finkeldey, R., Harahap, I., Hertel, D., Holtkamp, A. M., Hörandl, E., Irawan, B., Jaya, I. N. S., Jochum, M., Klarner, B., Knohl, A., Kotowska, M. M., Krashevska, V., Kreft, H., Kurniawan, S., Leuschner, C., Maraun, M., Melati, D. N., Opfermann, N., Pérez-Cruzado, C., Prabowo, W. E., Rembold, K., Rizali, A., Rubiana, R., Schneider, D., Tjitrosoedirdjo, S. S., Tjoa, A., Tscharntke, T., and Scheu, S.: Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes, Nat Commun, 7, 1–12, https://doi.org/10.1038/ncomms13137, 2016.

Clymans, W., Struyf, E., Govers, G., Vandevenne, F., and Conley, D. J.: Anthropogenic impact on amorphous silica pools in temperate soils, Biogeosciences, 8, 2281–2293, https://doi.org/10.5194/bg-8-2281-2011, 2011.

Clymans, W., Struyf, E., Van den Putte, A., Langhans, C., Wang, Z., and Govers, G.: Amorphous silica mobilization by inter-rill erosion: Insights from rainfall experiments, Earth Surf Process Landf, 40, 1171–1181, https://doi.org/10.1002/esp.3707, 2015.

Conley, D. J., Likens, G. E., Buso, D. C., Saccone, L., Bailey, S. W., and Johnson, C. E.: Deforestation causes increased dissolved silicate losses in the Hubbard Brook Experimental Forest, Glob Chang Biol, 14, 2548–2554, https://doi.org/10.1111/j.1365-2486.2008.01667.x, 2008.

Corley, R. H. v. and Tinker, P. B.: The Oil Palm, Fifth edit., 687 pp., https://doi.org/10.1017/cbo9781316530122.010, 2016.

Corley, R. H. v., Hardon, J. J., and Tan, G. Y.: Analysis of growth of the oil palm (Elaeis guineensis Jacq.) I. Estimation of growth parameters and application in breeding, Euphytica, 20, 307–315, https://doi.org/10.1007/BF00056093, 1971.

de Coster, G. L.: The Geology of the central and south sumatra basins, in: IPA, 2006 - 3rd Annual Convention Proceedings, 1974, 77, 2006.

Darras, K. F. A., Corre, M. D., Formaglio, G., Tjoa, A., Potapov, A., Brambach, F., Sibhatu, K. T., Grass, I., Rubiano, A. A., Buchori, D., Drescher, J., Fardiansah, R., Hölscher, D., Irawan, B., Kneib, T., Krashevska, V., Krause, A., Kreft, H., Li, K., Maraun, M., Polle, A., Ryadin, A. R., Rembold, K., Stiegler, C., Scheu, S., Tarigan, S., Valdés-Uribe, A., Yadi, S., Tscharntke, T., and Veldkamp, E.: Reducing Fertilizer and Avoiding Herbicides in Oil Palm Plantations—Ecological and Economic Valuations, Frontiers in Forests and Global Change, 2, 1–15, https://doi.org/10.3389/ffgc.2019.00065, 2019.

Datnoff, L. E., Deren, C. W., and Snyder, G. H.: Silicon fertilization for disease management of rice in Florida, Crop Protection, 16, 525–531, https://doi.org/10.1016/S0261-2194(97)00033-1, 1997.

Dislich, C., Keyel, A. C., Salecker, J., Kisel, Y., Meyer, K. M., Auliya, M., Barnes, A. D., Corre, M. D., Darras, K., Faust, H., Hess, B., Klasen, S., Knohl, A., Kreft, H., Meijide, A., Nurdiansyah, F., Otten, F., Pe'er, G., Steinebach, S., Tarigan, S., Tölle, M. H., Tscharntke, T., and Wiegand, K.: A review of the ecosystem functions in oil palm plantations, using forests as a reference system, Biological Reviews, 92, 1539–1569, https://doi.org/10.1111/brv.12295, 2017.

Drescher, J., Rembold, K., Allen, K., Beckscha, P., Buchori, D., Clough, Y., Faust, H., Fauzi, A. M., Gunawan, D., Hertel, D., Irawan, B., Jaya, I. N. S., Klarner, B., Kleinn, C., Knohl, A., Kotowska, M. M., Krashevska, V., Krishna, V., Leuschner, C., Lorenz, W., Meijide, A., Melati, D., Steinebach, S., Tjoa, A., Tscharntke, T., Wick, B., Wiegand, K., Kreft, H., and Scheu, S.: Ecological and socio-economic functions across tropical land use systems after rainforest conversion, Philosophical Transactions of the Royal Society B: Biological Sciences, 371, 20150275, https://doi.org/10.1098/rstb.2015.0275, 2016.

Dungani, R., Jawaid, M., Khalil, H. P. S. A., Jasni, Aprilia, S., Hakeem, K. R., Hartati, S., and Islam, M. N.: A review on quality enhancement of oil palm trunk waste by resin impregnation: Future materials, Bioresources, 8, 3136–3156, https://doi.org/10.15376/biores.8.2.3136-3156, 2013.

Epstein, E.: The anomaly of silicon in plant biology, Proceedings of the National Academy of Sciences, 91, 11–17, https://doi.org/10.1073/pnas.91.1.11, 1994.

Epstein, E.: Silicon: its manifold roles in plants, Annals of Applied Biology, 155, 155–160, https://doi.org/10.1111/j.1744-7348.2009.00343.x, 2009.

Euler, M., Hoffmann, M. P., Fathoni, Z., and Schwarze, S.: Exploring yield gaps in smallholder oil palm production systems in eastern Sumatra , Indonesia, Agricultural Sciences, 146, 111–119, https://doi.org/10.1016/j.agsy.2016.04.007, 2016a.

Euler, M., Schwarze, S., Siregar, H., and Qaim, M.: Oil Palm Expansion among Smallholder Farmers in Sumatra, Indonesia, J Agric Econ, 67, 658–676, https://doi.org/10.1111/1477-9552.12163, 2016b.

Gaveau, D. L. A., Locatelli, B., Salim, M. A., Husnayaen, Manurung, T., Descals, A., Angelsen, A., Meijaard, E., and Sheil, D.: Slowing deforestation in Indonesia follows declining oil palm expansion and lower oil prices, PLoS One, 17, e0266178, https://doi.org/10.1371/journal.pone.0266178, 2022.

Grass, I., Kubitza, C., Krishna, V. v., Corre, M. D., Mußhoff, O., Pütz, P., Drescher, J., Rembold, K., Ariyanti, E. S., Barnes, A. D., Brinkmann, N., Brose, U., Brümmer, B., Buchori, D., Daniel, R., Darras, K. F. A., Faust, H., Fehrmann, L., Hein, J., Hennings, N., Hidayat, P., Hölscher, D., Jochum, M., Knohl, A., Kotowska, M. M., Krashevska, V., Kreft, H., Leuschner, C., Lobite, N. J. S., Panjaitan, R., Polle, A., Potapov, A. M., Purnama, E., Qaim, M., Röll, A., Scheu, S., Schneider, D., Tjoa, A., Tscharntke, T., Veldkamp, E., and Wollni, M.: Trade-offs between multifunctionality and profit in tropical smallholder landscapes, Nat Commun, 11, 1–13, https://doi.org/10.1038/s41467-020-15013-5, 2020.

Grasshoff, K., Kremling, K., and Ehrhardt, M.: Methods of sea water analysis, third., John Wiley & Sons, 899 pp., https://doi.org/10.1016/0304-4203(78)90045-2, 2009.

Greenshields, B., von der Lühe, B., Hughes, H. J., Stiegler, C., Tarigan, S., Tjoa, A., and Sauer, D.: Oil-palm management alters the spatial distribution of amorphous silica and mobile silicon in topsoils, EGUsphere, 1–28, https://doi.org/10.5194/egusphere-2022-281, 2022.

Guntzer, F., Keller, C., Poulton, P. R., McGrath, S. P., and Meunier, J. D.: Long-term removal of wheat straw decreases soil amorphous silica at Broadbalk, Rothamsted, Plant Soil, 352, 173–184, https://doi.org/10.1007/s11104-011-0987-4, 2012.

Haynes, R. J.: A contemporary overview of silicon availability in agricultural soils, Journal of Plant Nutrition and Soil Science, 177, 831–844, https://doi.org/10.1002/jpln.201400202, 2014.

Haynes, R. J.: The nature of biogenic Si and its potential role in Si supply in agricultural soils, Agric Ecosyst Environ, 245, 100–111, https://doi.org/10.1016/j.agee.2017.04.021, 2017.

Heinrichs, H. and Hermann, A. G.: Praktikum der Analytischen Geochemie, in: Lehrbuch, Springer-Verlag, Berlin, 669, 1990.

Heinrichs, H., Brumsack, H. J., Loftfield, N., and König, N.: Verbessertes Druckaufschlußsystem für biologische und anorganische Materialien, Zeitschrift für Pflanzenernährung und Bodenkunde, 149, 350–353, 1986.

Hennings, N., Becker, J. N., Guillaume, T., Damris, M., Dippold, M. A., and Kuzyakov, Y.: Riparian wetland properties counter the effect of land-use change on soil carbon stocks after rainforest conversion to plantations, Catena (Amst), 196, 104941, https://doi.org/10.1016/j.catena.2020.104941, 2021.

Hughes, H. J., Hung, D. T., and Sauer, D.: Silicon recycling through rice residue management does not prevent silicon depletion in paddy rice cultivation, Nutr Cycl Agroecosyst, 118, 75–89, https://doi.org/10.1007/s10705-020-10084-8, 2020.

IUSS Working Group WRB: World Reference Base or Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps., FAO, Rome, 1–191 pp., https://doi.org/10.1017/S0014479706394902, 2022.

Klotzbücher, T., Klotzbücher, A., Kaiser, K., Merbach, I., and Mikutta, R.: Impact of agricultural practices on plant-available silicon, Geoderma, 331, 15–17, https://doi.org/10.1016/j.geoderma.2018.06.011, 2018.

Kotowska, M. M., Leuschner, C., Triadiati, T., Meriem, S., and Hertel, D.: Quantifying above- and belowground biomass carbon loss with forest conversion in tropical lowlands of Sumatra (Indonesia), Glob Chang Biol, 21, 3620–3634, https://doi.org/10.1111/gcb.12979, 2015.

Laumonier, Y.: The Vegetation and Physiography of Sumatra, in: Geobotany, vol. 22, Kluwer Academic Publishers, 223, https://doi.org/10.1007/978-94-009-0031-8, 1997.

Lewis, K., Rumpang, E., Kho, L. K., McCalmont, J., Teh, Y. A., Gallego-Sala, A., and Hill, T. C.: An assessment of oil palm plantation aboveground biomass stocks on tropical peat using destructive and non-destructive methods, Sci Rep, 10, 1–12, https://doi.org/10.1038/s41598-020-58982-9, 2020.

Li, Z. and Delvaux, B.: Phytolith-rich biochar: A potential Si fertilizer in desilicated soils, GCB Bioenergy, 11, 1264–1282, https://doi.org/10.1111/gcbb.12635, 2019.

Li, Z., de Tombeur, F., vander Linden, C., Cornelis, J. T., and Delvaux, B.: Soil microaggregates store phytoliths in a sandy loam, Geoderma, 360, 114037, https://doi.org/10.1016/j.geoderma.2019.114037, 2020.

Liang, Y., Nikolic, M., Bélanger, R., Gong, H., and Song, A.: Silicon in Agriculture, Dordrecht: Springer, 235 pp., https://doi.org/10.1007/978-94-017-9978-2, 2015.

vander Linden, C. and Delvaux, B.: The weathering stage of tropical soils affects the soil-plant cycle of silicon, but depending on land use, Geoderma, 351, 209–220, https://doi.org/10.1016/j.geoderma.2019.05.033, 2019.

Lucas, Y., Luizão, F. J., Chauvel, A., Rouiller, J., and Nahon, D.: The relation between biological activity of the rain forest and mineral composition of soils, Science (1979), 260, 521–523, 1993.

von der Lühe, B., Pauli, L., Greenshields, B., Hughes, H. J., Tjoa, A., and Sauer, D.: Transformation of Lowland Rainforest into Oil-palm Plantations and use of Fire alter Topsoil and Litter Silicon Pools and Fluxes, Silicon, 13, 4345–4353, https://doi.org/10.1007/s12633-020-00680-2, 2020.

von der Lühe, B., Bezler, K., Hughes, H. J., Greenshields, B., Tjoa, A., and Sauer, D.: Oil-palm and Rainforest Phytoliths Dissolve at Different Rates - with Implications for Silicon Cycling After Transformation of Rainforest Into Oil-palm Plantation, Silicon, https://doi.org/10.1007/s12633-022-02066-y, 2022.

Luke, S. H., Purnomo, D., Advento, A. D., Aryawan, A. A. K., Naim, M., Pikstein, R. N., Ps, S., Rambe, T. D. S., Soeprapto, Caliman, J.-P., Snaddon, J. L., Foster, W. A., and Turner, E. C.: Effects of understory vegetation management on plant communities in oil palm plantations in Sumatra, Indonesia, Frontiers in Forests and Global Change, 2, 1–13, https://doi.org/10.3389/ffgc.2019.00033, 2019.

Ma, J. F. and Takahashi, E.: Silicon-accumulating plants in the plant kingdom, in: Soil, fertilizer, and plant silicon research in Japan, Elsevier Science, Amsterdam, 63–71, https://doi.org/10.1016/b978-044451166-9/50005-1, 2002.

Meijaard, E., Brooks, T., Carlson, K. M., Slade, E. M., and Ulloa, J. G.: The environmental impacts of palm oil in context, Nat Plants, 6, 1418–1426, https://doi.org/10.1038/s41477-020-00813-w, 2020.

Munevar, F. and Romero, A.: Soil and plant silicon status in oil palm crops in Colombia, Exp Agric, 51, 382, https://doi.org/10.1017/S0014479714000374, 2015.

Ollivier, J., Flori, A., Cochard, B., Amblard, P., Turnbull, N., Syahputra, I., Suryana, E., Lubis, Z., Surya, E., Sihombing, E., and Gasselin, D. T.: Genetic variation in nutrient uptake and nutrient use efficiency of oil palm, J Plant Nutr, 40, 558–573, https://doi.org/10.1080/01904167.2016.1262415, 2017.

Omar, F. N., Mohammed, M. A. P., and Baharuddin, A. S.: Effect of silica bodies on the mechanical behaviour of oil palm empty fruit bunch fibres, Bioresources, 9, 7041–7058, https://doi.org/10.15376/biores.9.4.7041-7058, 2014.

Onoja, E., Chandren, S., Abdul Razak, F. I., Mahat, N. A., and Wahab, R. A.: Oil Palm (Elaeis guineensis) Biomass in Malaysia: The Present and Future Prospects, Waste Biomass Valorization, 10, 2099–2117, https://doi.org/10.1007/s12649-018-0258-1, 2019.

Pratiwi, W., Sugiharto, A., and Sugesty, S.: The effect of pulping process variable and elemental chlorine free bleaching on the quality of oil palm trunk pulp, Jurnal Selulosa, 8, 85, https://doi.org/10.25269/jsel.v8i02.218, 2018.

Puppe, D., Kaczorek, D., Schaller, J., Barkusky, D., and Sommer, M.: Crop straw recycling prevents anthropogenic desilication of agricultural soil–plant systems in the temperate zone – Results from a long-term field experiment in NE Germany, Geoderma, 403, 1–13, https://doi.org/10.1016/j.geoderma.2021.115187, 2021.

Qaim, M., Sibhatu, K. T., Siregar, H., and Grass, I.: Environmental, Economic, and Social Consequences of the Oil Palm Boom, Annu Rev Resour Economics, 12, 1–24, https://doi.org/10.1146/annurev-resource-110119-024922, 2020.

Rees, A. R.: The apical organization and phyllotaxis of the oil palm, Ann Bot, 28, 57–69, https://doi.org/10.1093/oxfordjournals.aob.a083895, 1964.

Rubinsin, N., Daud, W. R. W., Kamarudin, S. K., Masdar, M. S., Rosli, M. I., Samsatli, S., Tapia, J. F., Wan Ab Karim Ghani, W. A., and Lim, K. L.: Optimization of oil palm empty fruit bunches value chain in peninsular malaysia, Food and Bioproducts Processing, 119, 179–194, https://doi.org/10.1016/j.fbp.2019.11.006, 2020.

Saccone, L., Conley, D. J., Koning, E., Sauer, D., Sommer, M., Kaczorek, D., Blecker, S. W., and Kelly, E. F.: Assessing the extraction and quantification of amorphous silica in soils of forest and grassland ecosystems, Eur J Soil Sci, 58, 1446–1459, https://doi.org/10.1111/j.1365-2389.2007.00949.x, 2007.

Santi, L. P., Kalbuadi, D. N., and Goenadi, D. H.: Empty fruit bunches as potential source for biosilica fertilizer for oil palm, J Trop Biodivers Biotechnol, 4, 90–96, https://doi.org/10.22146/jtbb.38749, 2019.

Schaller, J., Turner, B. L., Weissflog, A., Pino, D., Bielnicka, A. W., and Engelbrecht, B. M. J.: Silicon in tropical forests: large variation across soils and leaves suggests ecological significance, Biogeochemistry, 140, 161–174, https://doi.org/10.1007/s10533-018-0483-5, 2018.

Selamat, M. E., Hashim, R., Sulaiman, O., Kassim, M. H. M., Saharudin, N. I., and Taiwo, O. F. A.: Comparative study of oil palm trunk and rice husk as fillers in gypsum composite for building material, Constr Build Mater, 197, 526–532, https://doi.org/10.1016/j.conbuildmat.2018.11.003, 2019.

Struyf, E., Smis, A., Van Damme, S., Garnier, J., Govers, G., Van Wesemael, B., Conley, D. J., Batelaan, O., Frot, E., Clymans, W., Vandevenne, F., Lancelot, C., Goos, P., and Meire, P.: Historical land use change has lowered terrestrial silica mobilization, Nat Commun, 1, 1–7, https://doi.org/10.1038/ncomms1128, 2010.

Tarigan, S., Stiegler, C., Wiegand, K., Knohl, A., and Murtilaksono, K.: Relative contribution of evapotranspiration and soil compaction to the fluctuation of catchment discharge: case study from a plantation landscape, Hydrological Sciences Journal, 65, 1239–1248, https://doi.org/10.1080/02626667.2020.1739287, 2020.

de Tombeur, F., Turner, B. L., Laliberté, E., Lambers, H., Mahy, G., Faucon, M. P., Zemunik, G., and Cornelis, J. T.: Plants sustain the terrestrial silicon cycle during ecosystem retrogression, Science (1979), 369, 1245–1248, https://doi.org/10.1126/science.abc0393, 2020.

Tsujino, R., Yumoto, T., Kitamura, S., Djamaluddin, I., and Darnaedi, D.: History of forest loss and degradation in Indonesia, Land use policy, 57, 335–347, https://doi.org/10.1016/j.landusepol.2016.05.034, 2016.

Vandevenne, F., Struyf, E., Clymans, W., and Meire, P.: Agricultural silica harvest: have humans created a new loop in the global silica cycle ?, Front Ecol Environ, 10, 243–248, https://doi.org/10.1890/110046, 2012.

Woittiez, L. S., van Wijk, M. T., Slingerland, M., van Noordwijk, M., and Giller, K. E.: Yield gaps in oil palm: A quantitative review of contributing factors, European Journal of Agronomy, 83, 57–77, https://doi.org/10.1016/j.eja.2016.11.002, 2017.

Woittiez, L. S., Slingerland, M., Rafik, R., and Giller, K. E.: Nutritional imbalance in smallholder oil palm plantations in Indonesia, Nutr Cycl Agroecosyst, 111, 73–86, https://doi.org/10.1007/s10705-018-9919-5, 2018.

Zellner, W., Tubaña, B., Rodrigues, F. A., and Datnoff, L. E.: Silicon’s Role in Plant Stress Reduction and Why This Element Is Not Used Routinely for Managing Plant Health, Plant Dis, 105, 2033–2049, https://doi.org/10.1094/PDIS-08-20-1797-FE, 2021.