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

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Abstract. Silicon (Si) is known to have multiple beneficial effects on crops. Most plant-available Si in 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, we hypothesized that i) Si is stored in the aboveground biomass of oil palms with time, and that ii) the system might lose considerable amounts of Si every year through fruit-bunch harvest. To test these hypotheses, we sampled leaflets, the rachis, fruit-bunch stalk, fruit pulp, kernels and frond bases from mature oil palms planted on well-drained and temporarily flooded riparian 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, leaflets of oil-palm fronds had a significantly higher ($p \leq 0.05$) mean Si concentration (≥ 1 wt. %) 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 store about 4 – 5 kg of Si in its total above-ground biomass, a smallholder oil-palm plantation of 1 hectare could store about 550 kg of Si in the palm trees' above-ground biomass. Pruned palm fronds were estimated to return 110 – 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 would occur 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, harvest, tropical soils

1 Introduction

Oil palms 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). Yet, well-balanced Si levels in soils are essential, as Si has several beneficial effects on crops, e.g., promoting the release of adsorbed macro-nutrients and preventing plant toxicity at low soil pH (Epstein, 2009; Schaller et al., 2020). Plants store Si in their leaf tissue. It strengthens their tissue, in this way mitigating biotic and abiotic stresses and reducing transpiration. Plants take up Si from soil solution as

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monomeric silicic acid (H_4SiO_4) (Haynes, 2017). Si is then transported from the roots to the shoot with the sap flow (Liang et al., 2015). Transpiration leads to an increase in Si concentration, and finally Si precipitates as amorphous silica bodies called phytoliths (SiO_2 * nH_2O) (Haynes, 2017; Liang et al., 2015). 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).

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). 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 (Epstein, 1994; Munevar and Romero, 2015). Munevar and Romero (2015) 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.

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 time to a degree that could negatively affect future 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 in oil-palm plantations differs from that 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), which is a key source of Si that can easily become plant-available. In oil-palm plantations, however, we expected Si 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 through harvest, as not only fruit but entire fruit bunches are removed from the system (Keller et al., 2012; Matichenkov and Calvert, 2002; Vandevenne et al., 2012). 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 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

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considered Si 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.

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 (Hennings et al., 2021; IUSS Working Group WRB, 2022). 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 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 at the well-drained sites (HO1 – 4) were 18 – 22 years old, and 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. The oil palms were planted in a triangular planting array with ~9 m distance between individual palm trees. Smallholder farmers followed common management practices. Thereby, interrows on either side of the oil-palm rows either served as harvesting paths or were used to stack pruned palm fronds (Darras et al., 2019). Herbicides (e.g., glyphosate) were sprayed biannually to clear understory vegetation in the interrows. The palm circle, a circular area with a radius of ca. 2 m around each oil-palm stem, where fertilizer is applied, (Munevar and Romero, 2015), was weeded regularly. Inorganic fertilizers (NPK, KCl and urea) were applied biannually within the palm circle (Allen et al., 2016; Euler et al., 2016).

2.2 Study design and plant sampling

To quantify Si concentrations in the different parts of an oil palm, and to subsequently derive Si storage estimates for the total above-ground biomass of the oil palms, we sampled leaflets, the rachis, fruit-bunch stalk, fruit pulp, the kernel, and frond bases of oil palms (Appendix, 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 (HOr – 4), three morphologically similar oil palms carrying at least one ripe fruit bunch were selected for sampling (Appendix, Table B2). 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 rachis and frond bases

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(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 not sample the oil-palm stems (Fig. 1b) and therefore refer to Pratiwi et al. (2018). 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 base for subsequent Si storage calculations.

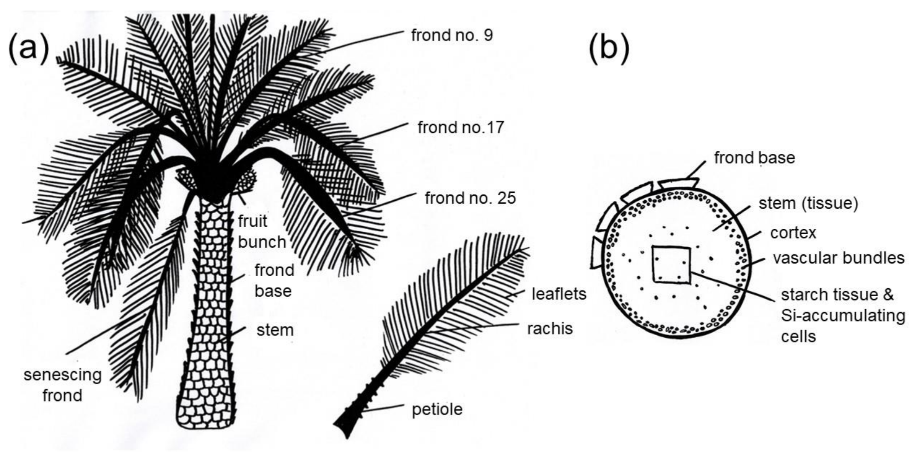

Fig. 1a Sketch of analysed oil-palm parts after Lewis et al. (2020).
Fig. 1b Sketch of cross-section through oil-palm stem, including Si-accumulating cells after Dungani et al. (2013)

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.

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). 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 according to Heinrichs et al. (1986) and Heinrichs and Hermann (1990). 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. 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 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, rachis, frond base, fruit-bunch stalk, fruit pulp and kernel (Section 2.2, Tab. 1a), but literature mostly provided dry weights of oil-palm main parts, i.e., stem with palm-frond bases, palm frond, palm crown and fruit bunch (Corley et al., 1971; Lewis et al., 2020), estimating Si storage in the above-ground biomas of oil-palms and 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. 1a). We then multiplied the dry biomass of each subpart by its Si concentration (Tab. 1b) to obtain 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. 1c). Si storage in the above-ground oil-palm biomass of 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 further distinguished between well-drained and riparian sites. Fruit-bunch biomass may vary noticeably among oil palms, whereas the other main parts, show less variability in their dry biomass. Therefore, dry biomass ranges are presented only for fruit bunches.

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Table 1a. Dry biomass estimates of main parts of mature oil palms in SE Asia and percentage relative contributions of subparts to the biomass of the main parts

Water regime[a]	Main oil-palm part	Biomass 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
[c]percentage 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 1b. Calculation of 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	Si concentrations [wt. %] in the contained subparts	Si storage in main oil-palm parts [kg][c]
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. (2016) 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]calculated by multiplying the 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

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Table 1c. 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 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 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
[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. 1c). Our estimates of Si return to soils were based on 14 – 16 pruned palm fronds per palm each year due to the average age of these oil palms (personal communication, A. Tjoa, Woittiez et al., 2017). Our 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 loss through fruit-bunch harvest. Again, these calculations were made 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 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 a line 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.

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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 rachis, frond base, fruit-bunch stalk, fruit pulp and kernel 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, Appendix, 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 rachis, which had a Si/Ca weight ratio of 0.5 (Appendix, 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, Appendix, 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 rachis, frond base, fruit bunch stalk, fruit pulp and kernel were in a similar range of around 0.3 to 0.5 wt. % Si (Fig. 2b). The rachis 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 (Appendix, 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, and no significant differences were detected (Appendix, 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).

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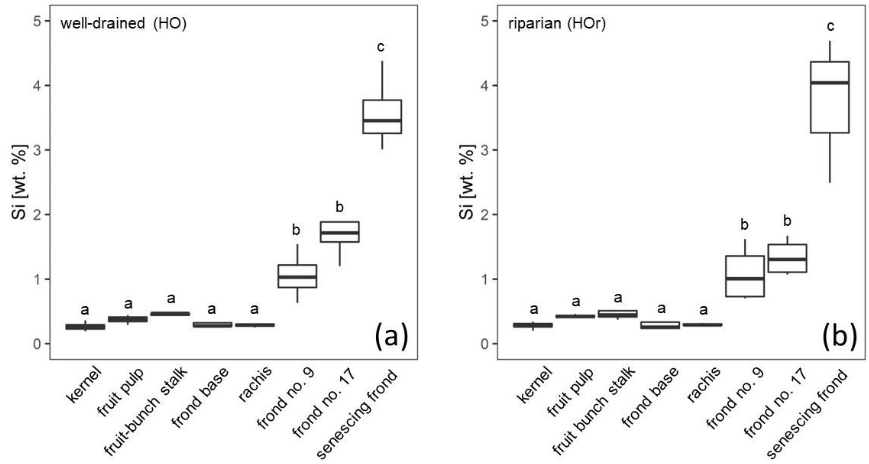

Fig. 2 Si concentrations in oil-palm subparts at well-drained (a) and riparian sites (b). Lower case letters indicate significant differences ($p \leq 0.05$) between oil-palm subparts within the same water regime.

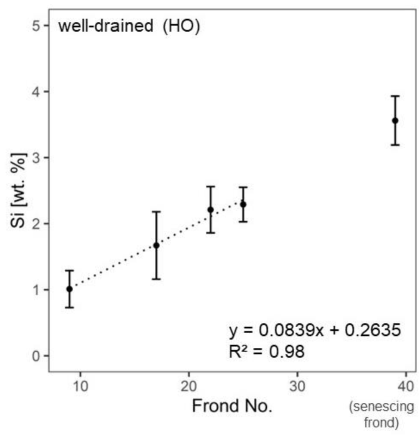

Fig. 3 Si concentrations in leaflets of five mature oil-palm fronds (no. 9, 17, 22, 25, senescing palm frond) from well-drained areas.

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

Table 1a 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 weigh between 5 kg and 20 kg (Appendix, Table B2).

Si storage in the analysed oil-palm parts was similar at well-drained and riparian sites (Tab. 1b). 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, 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. 1c). At well-drained sites, the above-ground biomass of a mature oil palm was estimated to store about 4 – 5 kg of Si. Consequently, oil palms in 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 110 kg per hectare. About 50 – 70 kg Si per hectare were lost by annual fruit bunch harvest in 2015, about 30 – 50 kg Si per hectare in 2018.

4 Discussion

4.1 Si distribution and accumulation in various oil-palm parts

In all palm leaflets, we found mean Si concentrations of ≥ 1 wt. % and a Si/Ca mass ratio of > 1. In addition, the Si concentration increased with leaf age. 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 (≥ 1 %) were significantly higher compared to all other above-ground oil-palm parts (≤ 0.8 %) (Fig. 2). This may be explained by Si preferentially precipitating at final transpiration sites, i.e., in the leaflets (Carey and Fulweiler, 2012). 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). In contrast to the leaflets, palm-frond bases and rachis are related to the transpiration stream rather than to transpiration and associated Si precipitation. 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 continues over the lifetime of an oil-palm frond, it results in a continuous increase of mean Si concentration in the leaflets with palm-frond age that 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), Si is either partly embedded within the surface, or precipitates directly on the surface of fruit-bunch fibres (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. In 2018, the yield was lower, with 9 – 14 Mg ha^{-1} dry biomass, corresponding to an Si export of 32 – 50 kg ha^{-1}.

According to Corley and Tinker (2016), 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 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

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-

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bunch harvest. This 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. 1a). 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 concentration in the stem (Tab. 1b) may seem negligible; yet, multiplying its Si concentration by the large stem biomass (accounting for 50 % of the entire oil-palm biomass; Aholoukpè et al., 2018) shows that the stem provides the largest Si pool of the oil palm's above-ground biomass. In contrast, palm leaflets show the highest Si concentrations (Tab. 1b) but contribute only 25 wt. % to the biomass of a palm frond. This leads 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. Thus, 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-palm plantations are usually cultivated for about 25 years (Corley and Tinker, 2016) after which the oil-palm stem is considered a waste product (Awalludin et al., 2015; Onoja et al., 2019). 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 (von der Lühe et al., 2020; Selamat et al., 2019). Yet, these nutrients, including Si, are released from the ash in such high amounts and so quickly that they are highly susceptible to leaching. It is likely that many nutrients are 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, air pollution, and to prevent fires from getting out of control and 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 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) (Pratiwi et al., 2018; Selamat et al., 2019) 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).

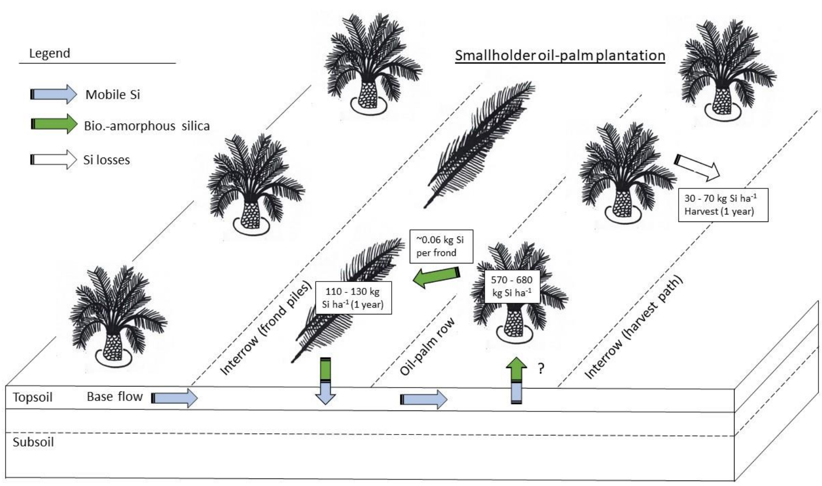

Fig. 4 Si storage in the above-ground biomass of oil palms, Si return to soils through decomposing pruned palm fronds, and Si losses through harvest on smallholder oil-palm plantations in Jambi Province, Sumatra.

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5 Conclusions

We conclude that the oil palm fulfils several criteria to be considered a Si accumulator (mean Si concentration ≥ 1 wt. % in leaflets, Si/Ca mass ratio ≥ 1, mean Si concentration increases with leaf age). A senescing frond stored 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 Si storage potential due to its high biomass when regarding Si storage of an oil palm 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.

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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

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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 No. 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

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

Oil-palm part	Water regime[b]	N	Total Si [%]			Ca [%]			Si/Ca ratio	Shapiro-Wilk p-value (ND)	Levene p-value (VAR)
			$\bar{x}$		σ	$\bar{x}$		σ			
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

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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.

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