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ORIGINAL ARTICLE

Environmental and farming practice controls of productivity of *Cyrtosperma merkusii* (giant swamp taro), an underutilised wetland and potential paludiculture crop

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Abstract

Growing recognition of the potential vulnerabilities of major crop systems has spurred a growing interest in the potential of alternative crops which may be resilient to climate change and also help mitigate its effects. In Indonesia, such issues are particularly pertinent given that country's particular vulnerability to climate change impacts high dependence on agricultural livelihoods and varied topographies and growing conditions. *Cyrtosperma merkusii* (giant swamp taro) is a wetland plant which has historically formed part of food systems in the eastern Pacific. The plant has the potential to be cultivated as a source of starch on marginal coastal land and on peatlands with high water tables. The aim of this paper was therefore to determine site conditions that promote growth of *C. merkusii* and the macro and micronutrient status of the corms. Naturally, the size of the plants varied substantially among sites, with a neutral pH, and low redox and conductivity being strong edaphic predictors of corm size. Despite substantial differences in the soil properties of the different study sites, there were no significant differences in the macro and micronutrient content of the corms. Field trials showed that although the plants grew under dry land conditions, the plants grew bigger and yielded corms with greater concentrations of Fe, Mn and K under waterlogged conditions, indicating that a high-water table is the best cultivation environment for *C. merkusii*. The nutrient content of the corms suggests that, although primarily a starch crop, *C. merkusii* could also increase the intake of Fe in populations where Fe deficiency is pervasive. We conclude that the wetland plant *C. merkusii* has considerable potential as a paludiculture crop in low-lying areas of SE Asia as it was tolerant of a wide range of soil conditions and performed well when cultivated under waterlogged conditions without additional fertilisation.

[Correction added on 18 October 2023, after first online publication: The corresponding author's name has been moved to the end of the author byline in this version.]

KEYWORDS
Cyrtosperma merkusii (giant swamp taro), paludiculture, sustainable agriculture, tropical, tuber crop, wetland

1 | INTRODUCTION

Balancing increases in food production with the need to safeguard the environment represents a major 21st century challenge, particularly in the tropics, where extremely rapid land use change is occurring (Miettinen et al., 2016; Taylor et al., 2009; Zhao et al., 2006). Indeed, land in SE Asia supports the food needs of large populations (ca 270 million people in Indonesia alone). Food security has been, and remains, a major component of public policy across the region, underpinning social and political stability, development trajectories as well as supporting large agricultural populations alongside growing urban middle- and working-class populations (Timmer, 2014). Historically, rice forms the mainstay of these policies. Indeed, for much of the 20th century the term "food security" was regarded as almost synonymous with rice production in the region. However, changing climate and socio-political conditions are increasingly undermining the viability of these approaches (Lebot, 2013; Mishra et al., 2021). Coastal areas in SE Asia in particular are facing multiple challenges linked to climate change, all of which have implications for food production. These include rising sea levels, subsidence, more intense storms resulting in coastal flooding and saltwater incursions (IPCC, 2021), intensified drought, and increasingly unpredictable weather patterns. While this situation raises issues at a global level, these coastal areas suffer disproportionate detrimental livelihood/food security, environmental and public health consequences from these climate change impacts (Shaw et al., 2022). In addition to the adverse effects of climate change itself, another issue that also must be considered is the shape of the proposed responses and efforts to mitigate them. Many of the costal and low-lying areas of southeast Asia, which are vulnerable to the effects of climate change, have also been identified as being of high importance in its mitigation, leading to calls for significant restrictions on the level and nature of human modification of these environments (Nabuurs et al., 2022). This may pose a particular problem to efforts to maintain these areas as centres for the intensive production of major crops which often requires significant intervention.

In this context interest has increased in exploring options to develop agri-food systems that can meet human food and livelihood needs and are resilient to variable climatic conditions while at the same time having fewer negative environmental impacts (Taylor et al., 2009). The wider use of underutilised crops is one such option. The term underutilised is applied to a wide range of plants which may be currently cultivated on a globally limited basis within specific communities and contexts (Jackson, 2008; Lebot, 2013). Such crops are often grown by small farmers living in remote areas where market access is limited, and in what would be considered to be marginal conditions for major crops (Jackson, 2008). For this reason, it has been suggested that these species may possess characteristics and adaptations which make them useful alternatives to major crops in areas where the latter cannot be successfully grown without major adaptations and extensive inputs. Identifying underutilised crops that are high yielding, nutritious, require low inputs and support a sustainable agri-environment (Jackson, 2008) and can be produced at scale offers one means of potentially delivering more resilient food systems, particularly in areas, which are environmentally sensitive and lack easy access to inputs (Lebot, 2013).

The importance of this paper thus lies in the urgent need to explore more underutilised crops for their potential as staple food sources that can ensure food security and sovereignty in the face of harsh environmental conditions arising from climate change while minimising the adverse climate and environmental impacts of cultivation (Jasrotia & Salgotra, 2021). *Cyrtosperma merkusii* (giant swamp taro) is a tuber crop found in the Pacific islands where it forms part of the diet (Englberger et al., 2008), suggesting that it has potential to make a contribution to regional food security (Lebot, 2013). The most compelling advantage of this taro species (note that *C. merkusii* is in a different genus compared to the more commonly grown *Coloclasia esculenta*) is that it can grow in brackish water, where the salinity of the soil can reach up to 1.5%, as well as a wide range of soil and moisture conditions (Englberger et al., 2008; Ragus & Sonis, 2016; Rao et al., 2014). This suggests that *C. merkusii* has potential as a food crop that is resilient to flooding and sea level incursion. Research on *C. merkusii*, from the Palau Islands to Singapore, have highlighted its current uses as a food crop and discussed its potential to address issues of food security while maintaining dietary diversity that is anchored in local traditions (Rao et al., 2014; Verma, 2016). In Micronesia, *C. merkusii* is an important local food and many defined local cultivars exist (Rao et al., 2014). In many of the locations were *C. merkusii* is eaten is it harvested from the wild on demand, rather than being deliberately cultivated (Jackson, 2008). However, in some areas *C. merkusii* is cultivated (e.g. Kiribati) and *C. merkusii*, together with other root crops, is part of the staple diet (Jackson, 2008; Ubaitoi, 1996). Further, corms are left to grow and are available to harvest year round, thus an additional feature of the crop that it is available as needed and storage requirements are minimal, effectively functioning as a living food reserve. Current cultivation practices are small-scale and labour-intensive and confined to the Pacific Islands. Some studies have investigated the nutritional proprieties (Bradbury et al., 1992; Nguimbou et al., 2014; Peng et al., 1993) others found considerable variation in Vitamin A and Zn, Ca and Fe concentrations (Englberger et al., 2008). There has also been some work towards developing food products from *C. merkusii* such as flours and rice analogues (Limbe et al., 2019) in line with work for other novel starch crops (Sede et al., 2015). However, although *C. merkusii* has the potential to be cultivated more widely as a flood-tolerant crop, further information is needed about preferred growing conditions and cultivation practices (Chauhan et al., 2022).

While most of the limited research that has been done on *C. merkusii* has been undertaken in the Pacific Islands, *C. merkusii* (Chauhan et al., 2022) is also utilised in North Sulawesi, Indonesia. Little is known about the role of *C. merkusii* as a food crop in Indonesia (Erlinawati et al., 2018; Limbe et al., 2019). On North Sulawesi *C. merkusii* are coastal plants growing in wetland or other coastal environments near the mangroves, and on islands in the far northern regions of Sulawesi, like the island of Siau and Sangihe, at 4°4′13″ N–4°44′22″ N and 125°9′28″ E–125°56′57″ E bordering North Sulawesi and Mindanao (Philippines), also the island of Talaud which lies at 4°5′31.2″ N and 126°46′4.8″ E (Figure 1; (Erlinawati et al., 2018). *Cyrtosperma merkusii* growing on Sangihe is mostly found in the interior of the island where the habitat is waterlogged and not impacted by saline conditions, while on Talaud *C. merkusii* grows closer to the shoreline in areas that are waterlogged only during the rainy season or after the seawater intrusive tide rises beyond the shoreline. Genetic work by Iese (2019) and Erlinawati et al. (2018) showed considerable genetic variation among *C. merkusii* plants from the different areas. Additionally to the genetic variation within the plants between Sangihe and Talaud, there is also considerable difference in how the plant is used is the two areas; *Cyrtosperma merkusii* on Sangihe island has been an important part of the indigenous culture, where these plants are left to grow naturally and not cultivated but play a role in the peoples' day-to-day life and in their traditions and culture as a snack food (Pers. Obs. Michelle Thomas M.), whereas the Talaud people use *C. merkusii* as animal feed, except for in Miangas (Northern Talaud) where *C. merkusii* is known as a staple replacement to rice (Pers. Obs. O'Reilly P. and Rahardiyan D.). In both islands, local farmers did not cultivate *C. merkusii*. Plants were harvested from time to time from their natural growth clusters and there was evidence that wild growth was encouraged, and plots safeguarded (Pers. Obs. Patrick O'Reilly and Dino Rahardiyan). Although local farmers are not cultivating *C. merkusii*, interviews confirmed corms are harvested and cooked in a sugar syrup as a snack food which is consumed within households and is sold at local markets. Its use as a staple food source by locals in times of drought, due to its resilience to harsh environmental conditions and year round availability was also recorded. This raises interest in the potential of *C. merkusii* as a more commonly cultivated and consumed crop and the need for improved understanding of its nutritional and cultivation requirements (Kurika, 1996).

The specific objectives of this study were to (1) assess growth habit, nutrient status and growth requirements of *C. merkusii* across North Sulawesi and surrounding islands delivering understanding of ecological requirements and resilience to flooding and salinity and (2) determine cultivation requirements to establish *C. merkusii* as a crop among local farmers and to optimize production systems.

2 | METHODS

2.1 | Field surveys

To address objective 1 we carried out field surveys in six separate locations where *C. merkusii* grew naturally. The sites were distributed across two islands Sangihe and Talaud with three sites selected on each island (Figure 1). Sites were selected based on *C. merkusii* patches being of sufficient size for the transect work, being close to the coast to understand impacts of salinity and spatially distributed. In each of the six sampling locations, four transects with four sampling locations on each transect were established, resulting in 16 sampling points in each location. Sampling points were ca 20–40 m apart depending on the size of the areas. At each sampling point we selected the three nearest plants to the transect point deemed to be of harvestable size (>15 cm diameter) by local farmers (Figure 2). At each sampling point a range of plant physiological parameters (e.g. leaf number and corm size) were collected to determine plant performance as well as a set of soil parameters (e.g. pH and redox). The sampling was carried out between September and December 2020 avoiding the severity of the rainy season.

Climatic conditions are humid tropical with a mean annual temperature of 28.2°C and mean annual precipitation of 3796 mm on Sangihe and a mean annual temperature of 26.5°C and mean annual precipitation of 3235 mm

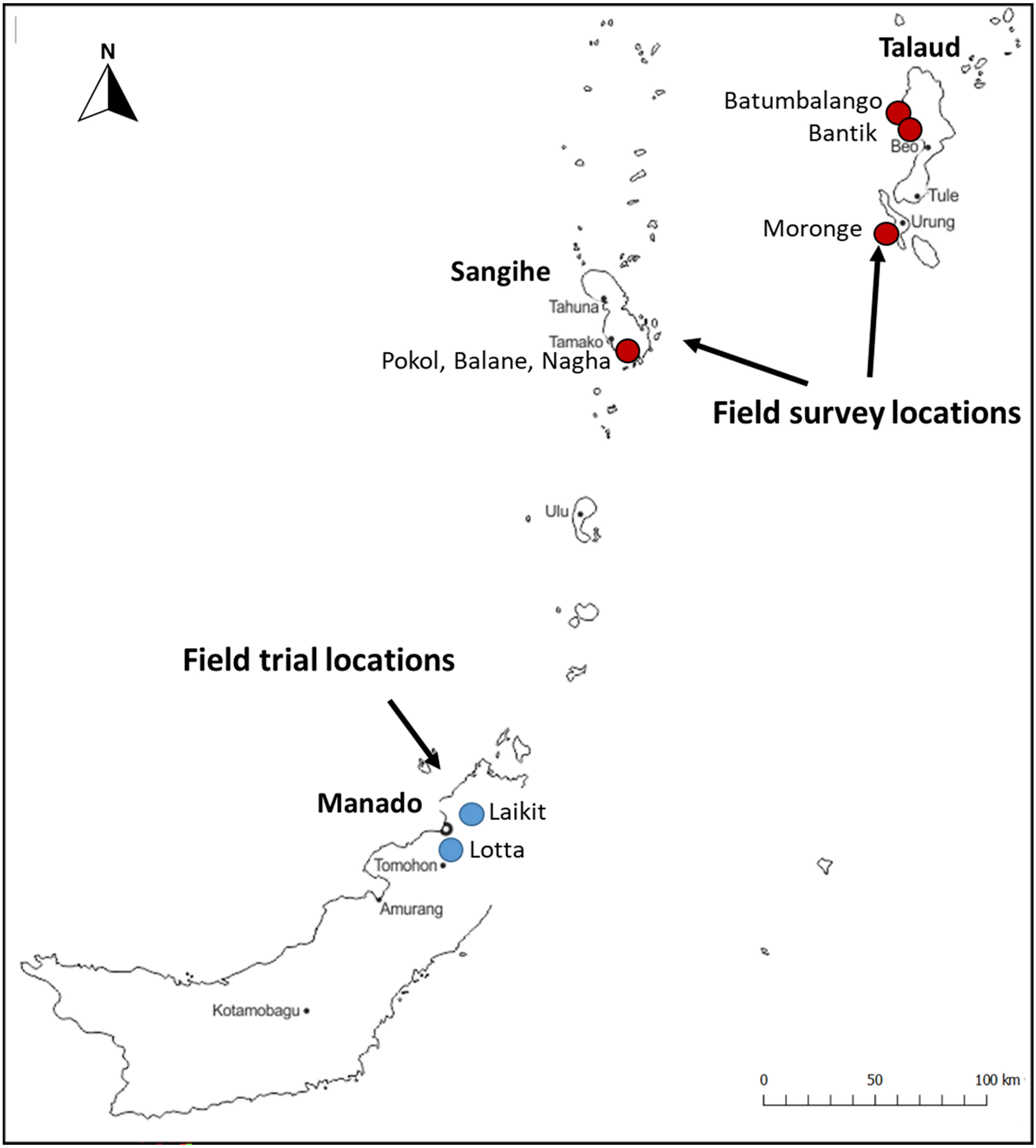

FIGURE 1 Map showing the location of the Sangihe and Talaud regencies, the location of the three field survey locations on each island (red dots, note that as sites where in the same region on Sangihe dots are overlapping). Manado, where the field trials were carried out in two locations (shown by blue dots), is also shown on the map.

on Talaud. All the sites were low lying with altitudes ranging between ca 10 and 25 m above sea level and close to the coast. The study areas varied somewhat in size and shape but were generally a few hundred metres long and wide and were located in waterlogged areas at low points in the local terrain. The soils varied among sites with peat and clay soils found at Sangihe while on Talaud *C. mercusii* grow in sandy soils. The islands used in the study are part of the Sangihe and Halmahera Island arc systems and have interior high-lying mountainous areas made up of strata of basalt, andesite, tectonic melange, and ophiolite (Moore et al., 1981).

FIGURE 2 Photos of *C. mercusii* growing at the two cultivation trial location on Manado and the size and cross section of corms.

2.2 | Plant and soil measurements

2.2.1 | Plant measurements

A range of plant trait measurements were collected for each selected plant. The stalk length of the tallest leaf was measured from the corm to the base of the leaf, stalk width was measured at 30 cm above the corm using a ruler. The leaf length from the point where stalk attached to the leaf and the leaf width were measured across the leaf at the point where the stalk attached to the leaf, the length of the leaf base was measured from where the stalk attached to the base of the leaf (Rao et al., 2013). Leaf greenness was recorded using a SPAD meter (SPAD-502 Plus, KONICA, Minolta Optics) for top, middle and lower leaves, eight SPAD readings were collected per leaf. For each plant the number of leaves was counted, and the number of flowers was recorded. The corm diameter and length were also recorded.

2.2.2 | Soil measurements

At each soil sampling point a ca 40 × 40 × 40 cm hole was dug, and the rooting depth measured, if it was greater than 40 cm this was recorded. We recorded if the soil were mainly organic (peat) or mineral and took a photograph of the soil profile from each sampling location. The majority of the sampling locations were waterlogged, and the resultant hole filled with water from the surrounding soil. We used this to measure pH, conductivity of redox in the soil solution after ca 30 min. Three repeated measurements of each parameter were taken.

2.2.3 | Nutrient analysis

Soil, leaf and corm samples were collected for nutrient analysis. For the soil analysis samples were collected from 0 to 15 and 15–30 cm depth, roots were removed from the soil samples prior to drying at 40°C. For the corm sample we cut out a segment of the corm (ca ¼), this sample was brought to the lab and washed, following washing the exposed surface of the corm was cut away removing any soil particles prior to drying. The leaf samples were washed in distilled water to remove any surface contamination and then dried before milling using a ball mill. Dried and milled samples were then prepared for analysis using microwave digestion and subsequently analysed for P, K, Mg, Mn, Fe, and Cu using inductively coupled plasma—optical emission spectrometry (ICP-OES) at SIG laboratories Bogor, Indonesia.

2.3 | Cultivation trials

To address objective 2 we carried out field trials cultivating *C. merkusii* in two contrasting growing environments. For this we collected plant material from three of the locations where we carried out the field surveys Sangihe (one location—Pokol) and Talaud (two locations, i.e. Bantik and Batambolango—subsequently referred to as Talaud-1 and Talaud-2 respectively). The use of source material from different areas in the trials was to understand if cultivation responses were reflected in the genetic variation in *C. merkusii* among source material from different areas (Erlinawati et al., 2018). The plant material that was collected were small, sprouted corms surrounding larger corms. For collection the small corms were carefully detached from the main corm and lifted from the soil using a spade. Following collection, the plants were placed on the ground under an agriculture shading net while keeping the plants moist and wet for 2 weeks. The plant material from the three source locations were subsequently cultivated for 12 months at two sites in Manado: Laikit (1°29′06″ N, 124°58′26″ E) and Sentrum Agraris Lotta (subsequently denoted LOTTA; 1°25′03″ N, 124°50′30″ E). The site at Laikit represented flooded (fresh water/waterlogged condition) growing conditions while the Lotta site was well drained. This allowed us to evaluate the difference in performance among the source material across waterlogged and relatively dry conditions. In addition, the plants were grown under three fertiliser regimes, control, inorganic fertiliser application and application of fermented pig manure with *Trichoderm* sp. bacteria consortium (known as *bokashi*, subsequently denoted "organic" fertiliser). The two fertilisers used were chosen as these are currently subsidised and available to farmers. The experiment used a split plot design organised in four replicate blocks with fertiliser on the main plot and source of planting material on the sub plot. Prior to the experiment, the site at Laikit had been used as a fresh water carp pond. This was excavated using diggers to remove residues from the fish farming and remodelled into three separate sections with 1 m soil mounds separating areas to allow for the fertiliser treatments without cross contamination. The water levels were maintained at 10–20 cm above the ground level. The Lotta site had previously been used for pasture. Prior to the experiment the site was carefully weeded by hand and prepared for planting. After the sites had been prepared the fertiliser treatment was applied, for the inorganic fertiliser treatment 3–5 g of nitrogen, phosphorus and potassium fertiliser (N:P:K; 20:20:20, the fertiliser also contained micronutrients such as Ca 0.05%, Mg 0.1%, S 0.2%, Cu 0.05% Mn 0.05%, Zn 0.05% Mo 0.0005% added to an inert material which constituted 39.0%) was added directly into the planting hole for each plant. For the organic fertiliser treatment, 300 g organic fertiliser was added in the planting hole of each plant. The corms were 2–3 cm diameter at the time of planting, and these were planted into holes of ca 20 cm diameter and 20 cm depth (Figure 2; Jackson, 2008). Following site preparation and fertilisation the corms were planted by hand, with 48 plants per plot. At the Lotta site the plants were watered after planting and thereafter daily using water from a nearby stream, at the Laikit site water was allowed to enter the site from a nearby stream after the plants were planted. The soils were sampled for nutrient analysis at the end of the experiment, further, soil redox, pH, conductivity and O_2 levels in the soil water were measured in situ at the Laikit site (but note at the Lotta site as there was no standing water at this site).

2.4 | Cultivation trial plant growth measurements and harvest

The growth of the plants in the cultivation trials was monitored over the 12-month growth period. A range of traits including, stalk length, stalk width, leaf length, leaf width and base length, leaf number, leaf greenness and corm diameter (following the same procedure as described for the plant surveys) were recorded every 2 weeks for the first 3 months after planting with a final set of data collected at the time of harvest after 12 months. At Laikit the leaf number data included both leaves on corms and suckers as it was difficult to distinguish between them in at the waterlogged site. Note that regular monitoring was not possible after month three due to Covid-19-related travel restrictions within Indonesia. At the end of the experiment the corms were harvested, and a subset of the corms were weighed ($n = 4$ per plot). Leaf and corm nutrient content were analysed alongside soil nutrients using the method described above.

2.4.1 | Data analysis

For the field survey we used residual maximum likelihood to test for significant differences between plant and soil parameters across the six different sites sampling locations; we used site (Balane, Nagha, Pokol, Batumbalango, Bantik and Moronge) as the fixed effect and island (Sangihe and Talaud) as the random effect using Genstat. Standard error of differences was used to identify differences between vegetation types and sites. For the field trial we used ANOVA to compare the impact of the treatments with site (Laikit or Lotta), source material (Sangihe, Talaud 1 or Talaud 2) and fertiliser (no fertiliser, inorganic and organic) as the fixed effect on the full range of plant parameters that were measured. To investigate which site properties were the best predictors of total biomass, corm size and corm weight we use stepwise backwards multiple regression. In instances where the data did not meet the model assumptions it was transformed using a log transformation.

3 | RESULTS

3.1 | Field survey

Plant size varied among sites. In general, the plants were ca. 1 m taller, had bigger (1 compared to 0.8 m wide) and more abundant leaves (ca five leaves on the biggest plants compared to three leaves on the smaller plants), as well as bigger corms (20 and 16 cm diameter, respectively) on the

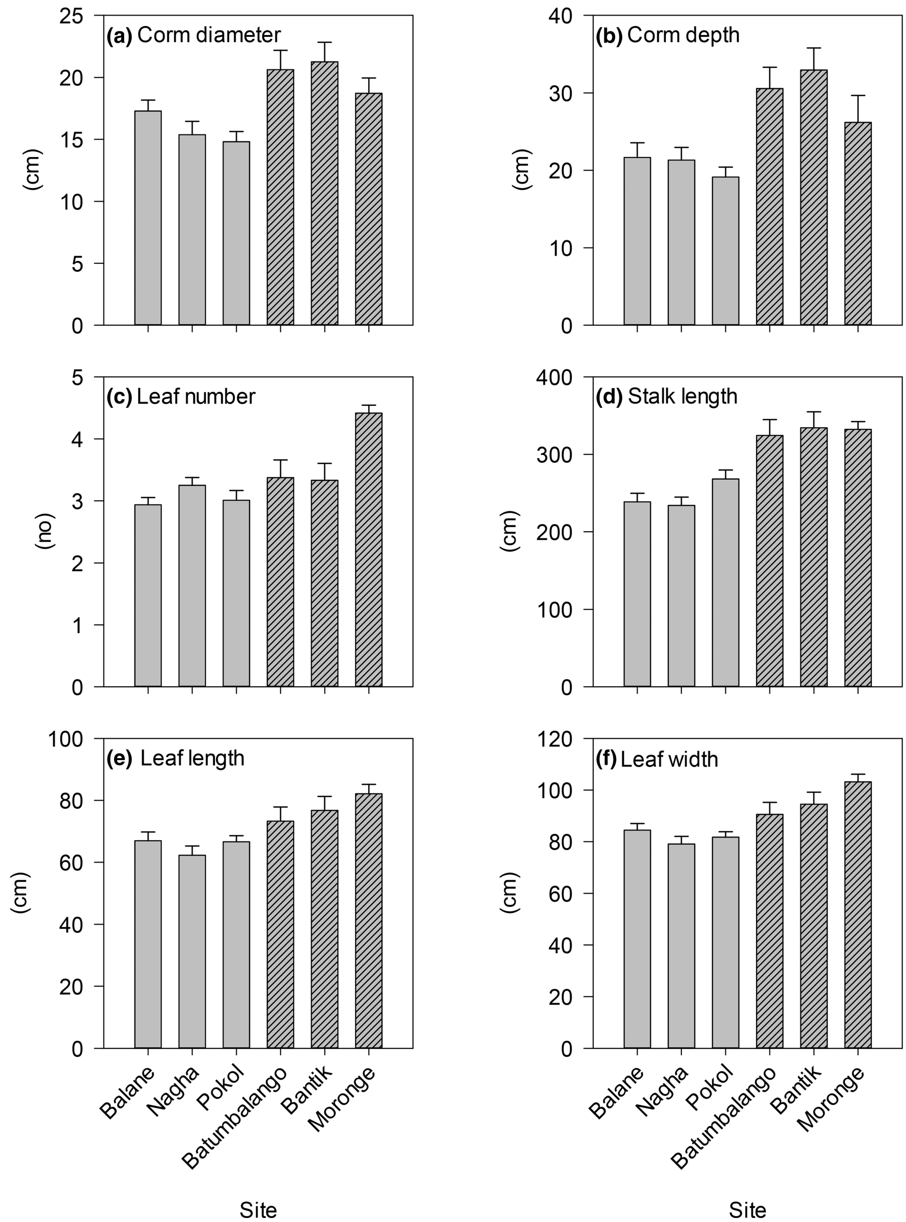

FIGURE 3 (a) Corm diameter, (b) corm depth, (c) leaf number, (d) stalk length, (e) leaf length, and (f) leaf width measured during the field survey at the six study locations, Balane, Nagha and Pokol are on Sangihe (plain grey bars) and Batumbalango, Bantik and Moronge are on Talaud (dashed bars). Means and SE are shown, the outputs of the statistical analysis are in Table 1.

sites at Talaud than Sangihe (Figure 3; Table 1). SPAD values were in the range of 50–60 for the upper leaves while for the lower leaves it ranged around 30–40 (Figure 4); The highest SPAD values were found at the Pokol and Moronge sites (Figure 4; Table 1).

3.2 | Soil properties and nutrient variation across sites

Redox status (an indicator of water logging) varied among sites with four of the six having a negative redox status showing anoxic condition (Tables 1 and 2). The pH levels also differed among sites, being above 7 at Bantik, Moronge and Batumbalango and varying between 6 and 7 at the remaining sites. The soil pH for the most part was negatively associated with redox profile and the three

TABLE 1 Statistics comparing differences in plant and soil parameters among the six field survey sites.

Parameter	Fixed effect	df	*F*	*p*
Stalk length	Site	5, 90	10.11	<0.001
Leaf width	Site	5, 90	6.67	<0.001
Leaf number	Site	5, 90	5.71	<0.001
SPAD	Site	3, 165	5.77	<0.001
Corm diameter	Site	5, 90	4.69	<0.001
Redox	Site	5, 64	229.68	<0.001
pH	Site	5, 66	110.57	<0.001
Conductivity	Site	5, 64	6.88	<0.001
Water table	Site	5, 66	10.1	<0.001
Soil temperature	Site	5, 66	21.9	<0.001
O_2	Site	5, 66	63.03	<0.001

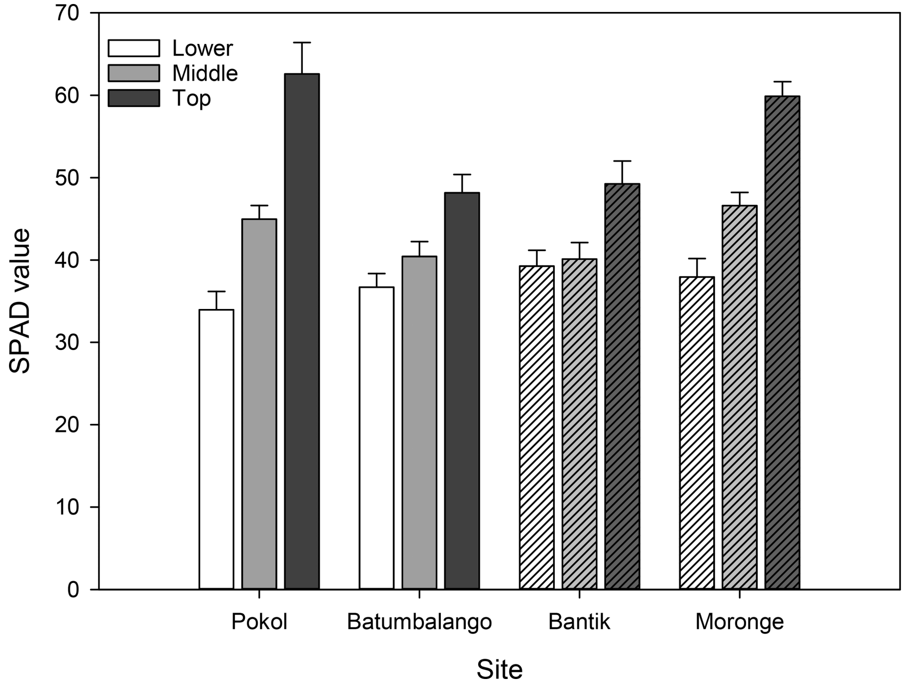

FIGURE 4 Leaf SPAD value according to leaf position on the plant (i.e. Lower, middle and top leaves were measured) at four of the field survey study sites (data was not collected from Balane and Nagha). The undashed bars are from sites in Sangihe and dashed bar are from Taluad. Mean and SE are shown.

TABLE 2 Soil properties measured in the soil pore water at the six field survey locations and the Laikit field trial site.

Site	O_2 (mg/L)		pH		Redox (mV)		Soil T °C		Water table depth (cm)		Conductivity (µS)	
Balane	1.52	±0.01	6.08	±0.02	58.9	±0.69	25.7	±0.1	13	±1	69.9	±1.1
Nagha	2.07	±0.03	6.44	±0.04	33.4	±0.65	25.8	±0.1	28	±2	118.4	±1.5
Pokol	1.17	±0.03	6.67	±0.03	−87.1	±11.65	26.2	±0.1	27	±2	83.8	±3
Batumbalango	0.85	±0.03	7.67	±0.10	−228.6	±7.95	26.5	±0.1	21	±2	321.7	±32.1
Bantik	0.88	±0.03	7.72	±0.10	−223.5	±11.78	26.6	±0.1	22	±2	349.9	±20.8
Moronge	ND	±0.03	7.68	ND	−272.0	ND	26.5	±0.1	28	ND	360.3	ND
Laikit (trial)	1.56	±0.04	6.96	±0.09	−204.2	±6.85	28.8	±0.4	[a]		139.9	±12.39

Note: Means and SE are shown. There was no standing water in the soil at the second field trial site, Lotta, which is why data for this site is not included.

[a]The water table was maintained at ca 15 cm above the ground surface throughout the trial.

sites with pH above 7 all had redox levels below -200 µS. Further, Bantik, Moronge and Batumbalango had high conductivity values (ca 300–450 µS) most likely linked to some tidal influence at these sites. The other sites had conductivity values around 100 µS, indicating that those sites were not experiencing influence from the marine system.

3.2.1 | Links between soil and plant properties and corm size

Stepwise backward multiple regression analysis which included all plant and soil explanatory in the maximal model showed that corm diameter was best predicted by leaf length, leaf number and soil pH ($F_{3,36}=31.77$, $\sigma^2=64\%$). The significant single linear relationships between corm diameter and explanatory variables are shown in Figure 5. Of these, pH was the strongest single predictor of corm size, with larger corms found in plots with higher pH (Figure 5). The relationship between pH and redox is also shown to illustrate the collinearity between these two parameters.

3.3 | Corm nutrient content

Corm nutrient content ranged between 437 to 664 mg P kg^{-1}, 6738 to 16,471 mg K kg^{-1}, 461 to 781 mg Mg kg^{-1}, 20 to 33 mg Fe kg^{-1}, 145 to 496 mg Mn kg^{-1} and 1.5 to 12 mg Cu kg^{-1} (Table 3). The corm nutrient content did not vary among sites for any of the analysed nutrients ($p>0.05$). Soil Mg concentration was the only soil nutrient parameter that was related to corm size ($F_{1,94}=11.89$, $p<0.001$, $\sigma^2=10.3\%$), however, adding soil Mg to the regression model predicting corms size reported above did not improve the model.

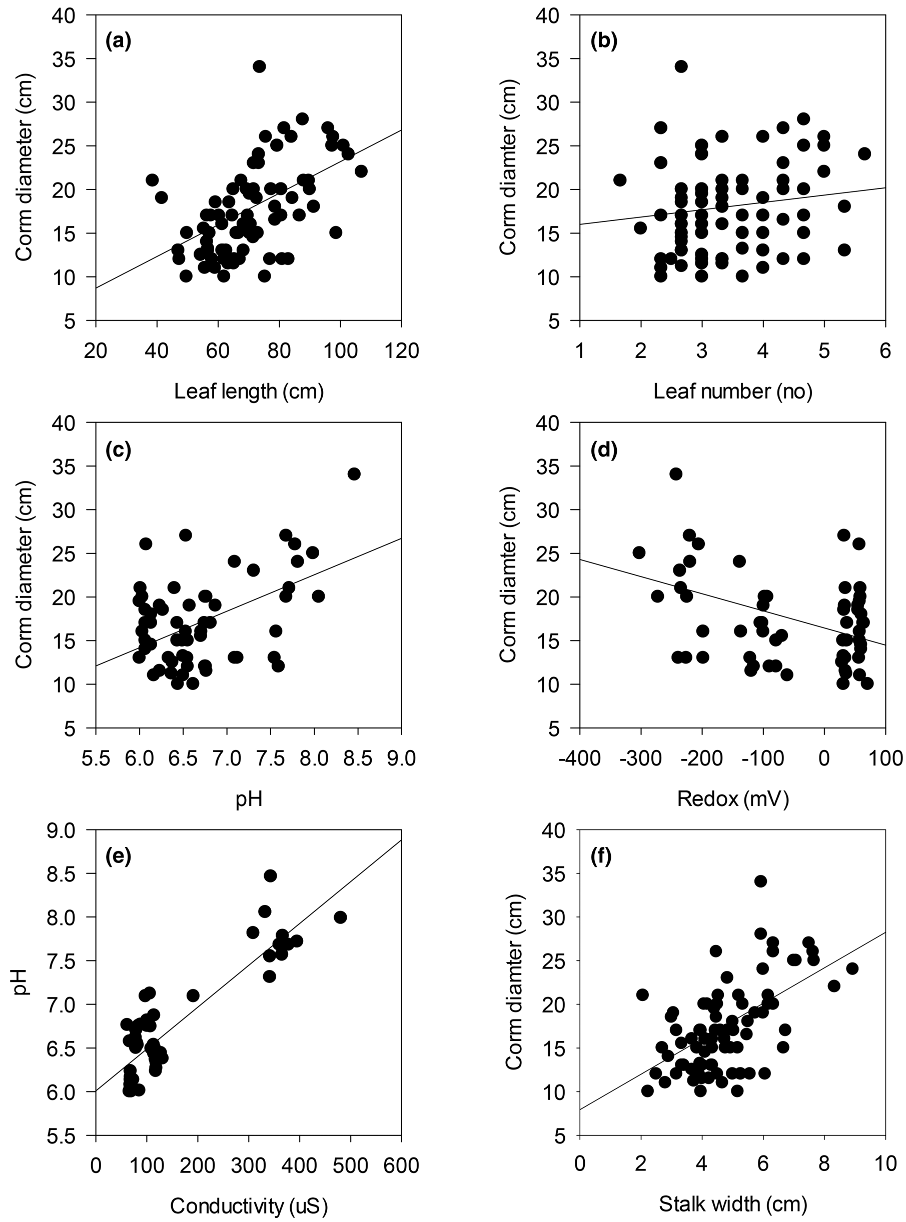

FIGURE 5 Relationships between (a) leaf length and corm diameter $F_{1,62}=48.48$; $p<0.001$, $\sigma^2=54.9$; (b) leaf number and corm diameter $F_{1,62}=0.07$, $p=0.8$; (c) pH and corm diameter $F_{1,38}=48.48$; $p<0.001$, $\sigma^2=54.9\%$; (d) redox and corm diameter $F_{1,38}=20.45$, $p<0.001$, $\sigma^2=33.3$; (e) conductivity and pH $F_{1,38}=158.24$, $p<0.001$, $\sigma^2=80.1$; and (f) stalk width and corm diameter $F_{1,62}=24.21$, $p<0.001$, $\sigma^2=26.9$ based on data from the field surveys at six sites. The statistics and regression lines refer to single linear regression models.

3.4 | Field trial

Over the time course of the field trials the non-destructive measurements of plant growth showed that the plants developed larger leaves, greater number of leaves, longer and wider stems at the water-logged site (Figures 5 and 6; Table 4). Furthermore, a significant interaction between site and fertiliser treatment highlighted that the impact on leaf length, leaf width and stalk length from the fertilisers differed between the Laikit and the Lotta sites.

At the end of the experiment the majority of plant parameters showed a significant interaction between site*-fertiliser linked to reduced plant performance in plots receiving inorganic fertiliser at the water-logged Laikit site but not at the Lotta site (Figure 7; Table 4). There was no significant impact of the treatments on SPAD values at the Lotta site either in the first 3 months after planting, or at the time of harvest, at which time values were 38.8 ± 0.89, 38.0 ± 0.9, and 37.3 ± 0.6, in control, inorganic and organic treatments respectively. At the Laikit site SPAD values differed among source material with the highest SPAD values at the time of harvest found for Talaud 1 source material, followed by the Sangihe and Talaud 2 source material with values of 41.7 ± 1.0, 35.1 ± 0.9, and 23.5 ± 0.9, respectively ($F_{2,18}=93.24$, $p<0.001$) but not fertiliser application.

At the end of the 12 month experiment, corm diameter ranged between 4 and 8 cm with a mean of 5.1 ± 0.3 and 5.3 ± 0.5 cm at the Laikit and Lotta site, respectively. The fresh weight ranged between 300–400 g plant^{-1}. In addition to the main corm the plants produced suckers with 4 ± 0.5 and 8 ± 0.9 suckers per plant at the Lotta and Laikit site respectively. Leaf length and stalk length were overall greater at the Laikit site (Figure 8). This site also

TABLE 3 Nutrient content in soil, leaves and corm at the six field survey sites.

Tissue	Site: Balane		Nagha		Pokol		Batumbalango		Bantik		Moronge	
P (mg/kg)												
Soil	300	±24	312	±36	343	±30	388	±40	462	±73	1713	±59
Leaves	1872	±90	1779	±47	1916	±55	2240	±63	224	±76	1546	±43
Corm	664	±75	437	±39	591	±44	506	±86	474	±20	nd	
K (mg/kg)												
Soil	347	±905	267	±29	266	±36	604	±34	1392	±227	475	±69
Leaves	26,537	±1557	29,321	±970	19,909	±2619	29,613	±1692	31,245	±700	18,726	±1120
Corm	10,559	±1708	9884	±1098	11,193	±1142	6738	±983	16,471	±4073	nd	
Mg (mg/kg)												
Soil	1259	±356	476	±29	787	±35	4363	±253	6527	±428	654	±27
Leaves	6666	±189	5500	±163	5630	±239	6989	±126	5644	±167	4212	±167
Corm	781	±68	461	±38	553	±26	576	±61	619	±75	nd	
Fe (mg/kg)												
Soil	7044	±1031	20,109	±2911	8478	±944	12,059	±750	18,770	±1045	4161	±325
Leaves	85	±4	78	±3	78	±5	101	±3	63	±5	58	±2
Corm	33	±5	20	±4	21	±3	25	±4	28	±6	nd	
Mn (mg/kg)												
Soil	115	±20	448	±87	87	±14	193	±54	1586	±568	203	±33
Leaves	2389	±213	2412	±116	2295	±137	2522	±180	7340	±626	851	±93
Corm	149	±29	155	±24	145	±12	203	±31	496	±58.	nd	
Cu (mg/kg)												
Soil	38	±2	43	±2	62	±4	35	±2	50	±2	36	±1
Leaves	19	±1	15	±1	18	±1.	16	±1	17	±1	16	±1
Corm	4.7	±2.6	12.6	±1.1	6	±2.7	1.5	±0.7	8.5	±3.3	nd	

Note: Mean and SE are shown.

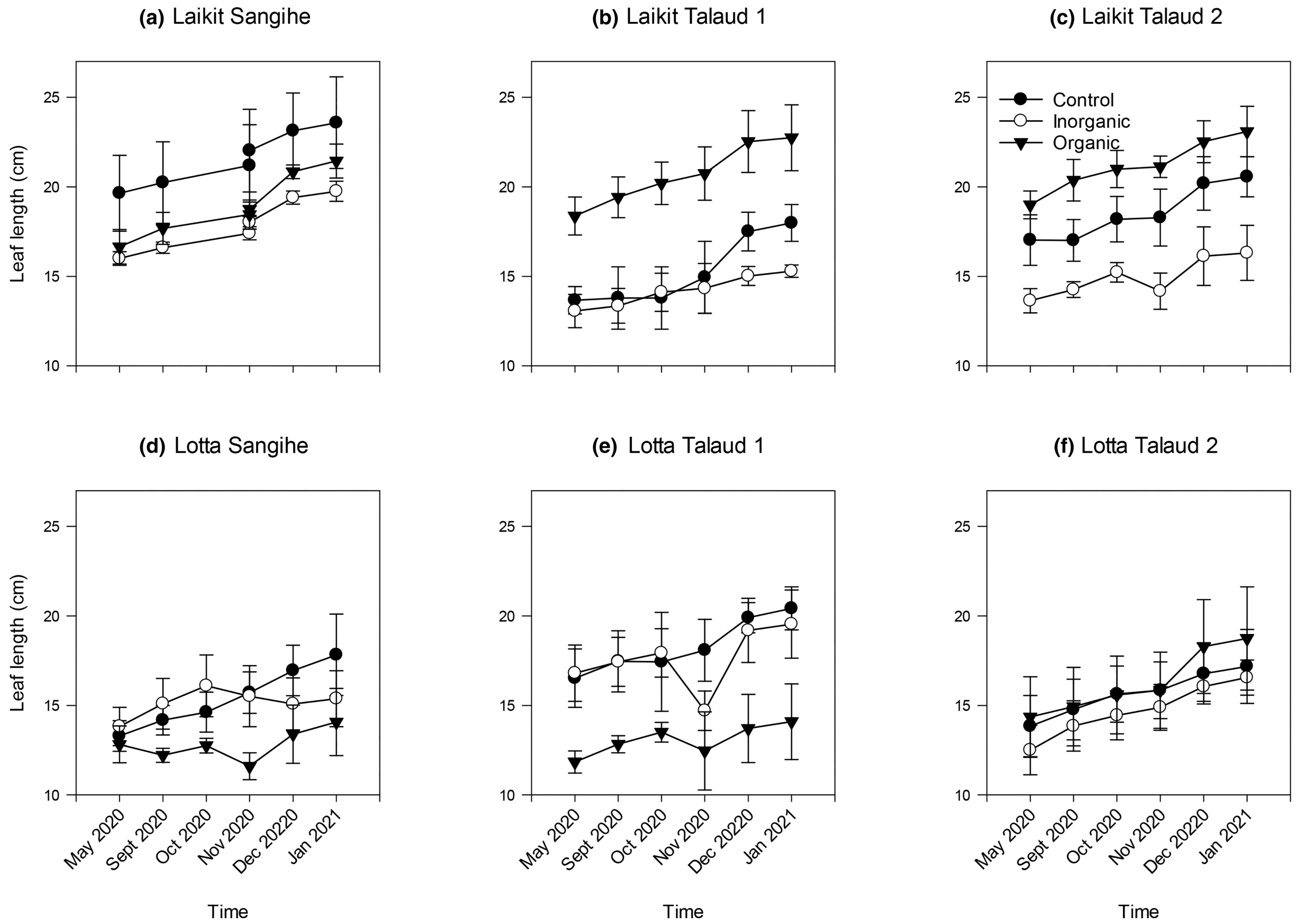

FIGURE 6 Data from the field trial on leaf length measured in response to site, fertiliser treatment and source material at six time points over the 12-month experiment in (a–c) the Laikit site and (d–f) the Lotta site for the source materials originating from (a, d) Sangihe, (b, e) Talaud 1, (c, f) Talaud 2. Means and SE are shown.

saw a positive impact of the organic fertiliser treatment on plant growth. Under control conditions at this site the source material from Sangihe outperformed the source material from Talaud. In contrast, there was no significant difference in control plots in either above or corm biomass between the two sites and there was no overall impact of fertiliser application (Figure 9; Table 5). The negative impact of the inorganic fertiliser on plant growth at the Laikit site (Figure 6a–c) translated into reduced above and below-ground biomass at this site (Figure 9b; Table 5).

There was a significant linear relationship between corm diameter and corm biomass ($F_{1,23}=11.2$, $p<0.01$, $\sigma^2=29.8$) as well as between stalk length and corm biomass ($F_{1,52}=7.58$, $p<0.01$, $\sigma^2=11.0$) suggesting that these two parameters were good indicators of the weight of the corm (Figure 10).

Soil nutrient content of P, K, Mg, Mn, Fe, and Cu were consistently greater at the Lotta than Laikit site at the time of the biomass harvest (Table 6).

Leaf Fe and Mn content was higher at the flooded site while leaf Mg, P and K content were greatest at the Lotta site (Table 7). For the corms, Fe, Mn and K content were higher at the Laikit site while P content was higher in the corms at the well-drained site. Cu and Mg content in corms did not differ between sites (Supplementary Information S1).

4 | DISCUSSION

Cytosperma merkusii was found in areas exhibiting a range of water table levels showing that the plant is adaptive to a range as well as fluctuating of water levels. Further, *C. merkusii* corms grew bigger and had higher SPAD values (Colombo et al., 2018) under negative redox conditions associated with flooded soils in neutral/slightly alkaline soil in coastal areas suggesting that the plant performed best in waterlogged conditions. Together, this indicates that *C. merkusii* has potential as a wetland crop. *C. merkusii* is considered a salt tolerant plant (Ragus & Sonis, 2016), however, none of the North Sulawesi study locations showed saline conditions with

TABLE 4 Statistics comparing differences in plant parameters linked to the treatments over the course of the field trial at the two sites, Laikit and Lotta.

Parameter	Factor	df	*F*	*p*
Leaf number	**Site**	**1, 28**	**63.54**	**<0.001**
	Source material	2, 28	0.85	0.437
	Fertiliser	2, 28	3.31	0.051
	Site × source material	2, 28	0.85	0.439
	Site × fertiliser	2, 28	2.43	0.106
	Source material × fertiliser	4, 28	0.92	0.464
	Site × source material × fertiliser	4, 28	0.98	0.433
Leaf width	**Site**	**1, 31**	**12.43**	**0.001**
	Source material	2, 31	1.99	0.153
	Fertiliser	**2, 31**	**3.67**	**0.037**
	Site × source material	**2, 31**	**5.14**	**0.012**
	Site × fertiliser	**2, 31**	**6.66**	**0.004**
	Sourcematerial × fertiliser	4, 31	1.21	0.327
	Site × source material × fertiliser	4, 31	2.07	0.108
Leaf length	**Site**	**1, 30**	**13.17**	**0.001**
	Source material	2, 30	0.08	0.919
	Fertiliser	2, 30	2.38	0.109
	Site × source material	**2, 30**	**3.31**	**0.050**
	Site × fertiliser	**2, 30**	**5.77**	**0.007**
	Source material × fertiliser	4, 30	1.30	0.291
	Site × source material × fertiliser	4, 30	1.89	0.137
Stalk length	**Site**	**1, 37**	**20.57**	**<0.001**
	Source material	2, 37	0.48	0.622
	Fertiliser	**2, 37**	**5.21**	**0.010**
	Site × source_material	**2, 37**	**4.93**	**0.013**
	Site × fertiliser	**2, 37**	**8.04**	**0.001**
	Source material × fertiliser	4, 37	1.05	0.394
	Site × source material × fertiliser	4, 37	1.48	0.228
Stalk width	**Site**	**1, 23**	**28.55**	**<0.001**
	Source material	2, 23	0.73	0.494
	Fertiliser	2, 23	1.68	0.207
	Site × source material	2, 23	0.60	0.557
	Site × fertiliser	2, 23	0.36	0.701
	Source material × fertiliser	4, 23	0.20	0.933
	Site × source material × fertiliser	4, 23	0.97	0.443

Bold values indicate statistically significant effect.

the upper conductivity range measured at the study sites being ca 400 µS. This demonstrates that *C. merkusii* is not confined to coastal wetlands but also grows well in fresh water wetlands across a range of pH values including in mildly acid soils.

The varying soil conditions among the survey sites did not translate to differing corm nutrient content suggesting that the soil conditions in which these plants grew naturally did not drive differences in nutrient content in corms of harvestable size. However, the corm Fe content was higher (at 21 to 33 mg/kg) than levels reported from Micronesia and Palau (3 to 8 mg/kg; Englberger et al., 2008). This suggests that although we did not identify strong link between soil and corm nutrient content, corm Fe content can be variable among locations. This is important from a nutritional perspective as low iron status has been seen in local populations in recent years, with high prevalence of anaemia (Knijff et al., 2021) (Mansyur et al., 2019). The iron content of C. *merkusii* seen in our study may potentially represent

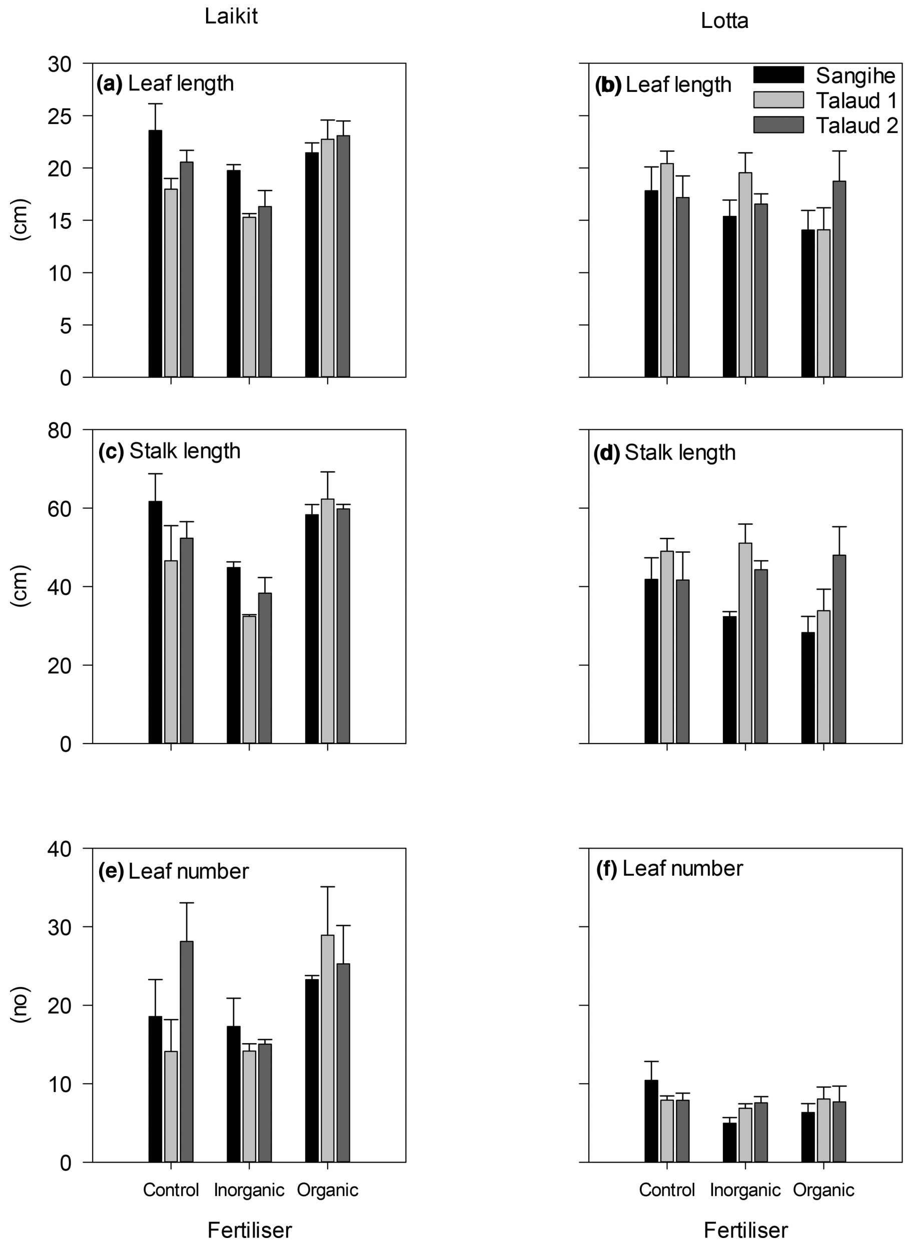

FIGURE 7 Data at harvest time from the field trial showing the impact of the fertiliser treatment and source material on (a) Leaf length at the Laikit site, (b) Leaf length at the Lotta site, (c) Stalk length at the Laikit site (d) Stalk length at the Lotta site, (e) Leaf number at the Laikit site and (f) Leaf number at the Lotta site. Mean and SE is shown.

a novel and significant source of iron in the diet at the higher end (Fe content of different cultivars have been found to range from 6 to 36 mg/kg; (SPC., 2006) and high flour Fe content of 72.0 mg/kg (Limbe et al., 2019). This is high compared to other staple sources of carbohydrate such as rice, yams and potatoes between 4.5 and 6.5 mg/kg (Bielecka et al., 2021), 3.5–15.2 $mg\,kg^{-1}$ (Adepoju et al., 2018) and 2.2–10.5 $mg\,kg^{-1}$ (Ariza-Nieto et al., 2006, 2007) respectively. Replacement of these foods with swamp taro could potentially increase Fe provision up to three-fold if content can be consistently ensured and low levels of anti-nutrients preventing absorption (e.g. phytates) are present. Indeed, it would be important to ascertain levels of anti-nutritional factors to ensure low levels as well as identifying processing steps that can be adopted to reduce their concentrations to safe limits if present prior to *C. merkusii* forming a greater proportion of the diet.

The field trials demonstrated that C. *merkusii* could be successfully grown as crop yielding 4–8 cm diameter corms after 12 months. It was also clear that above-ground biomass grew best in waterlogged soil conditions similar to those in which the plants grew. Although our trials did not show site differences in yield after 12 months we anticipate these would manifest following a longer growth period in line with the findings from the field survey where larger plants had bigger corms. Indeed, in the locations where farmers collected *C. merkusii* from the wild, plants were allowed to grow for ca 2–3 years and have a corm diameter of ca 15–20 cm when harvested (Englberger et al., 2008). Further, Rao et al. (2014) report ca 15 different cultivars of *C. merkusii* in Micronesia and Erlinawati et al. (2018) report

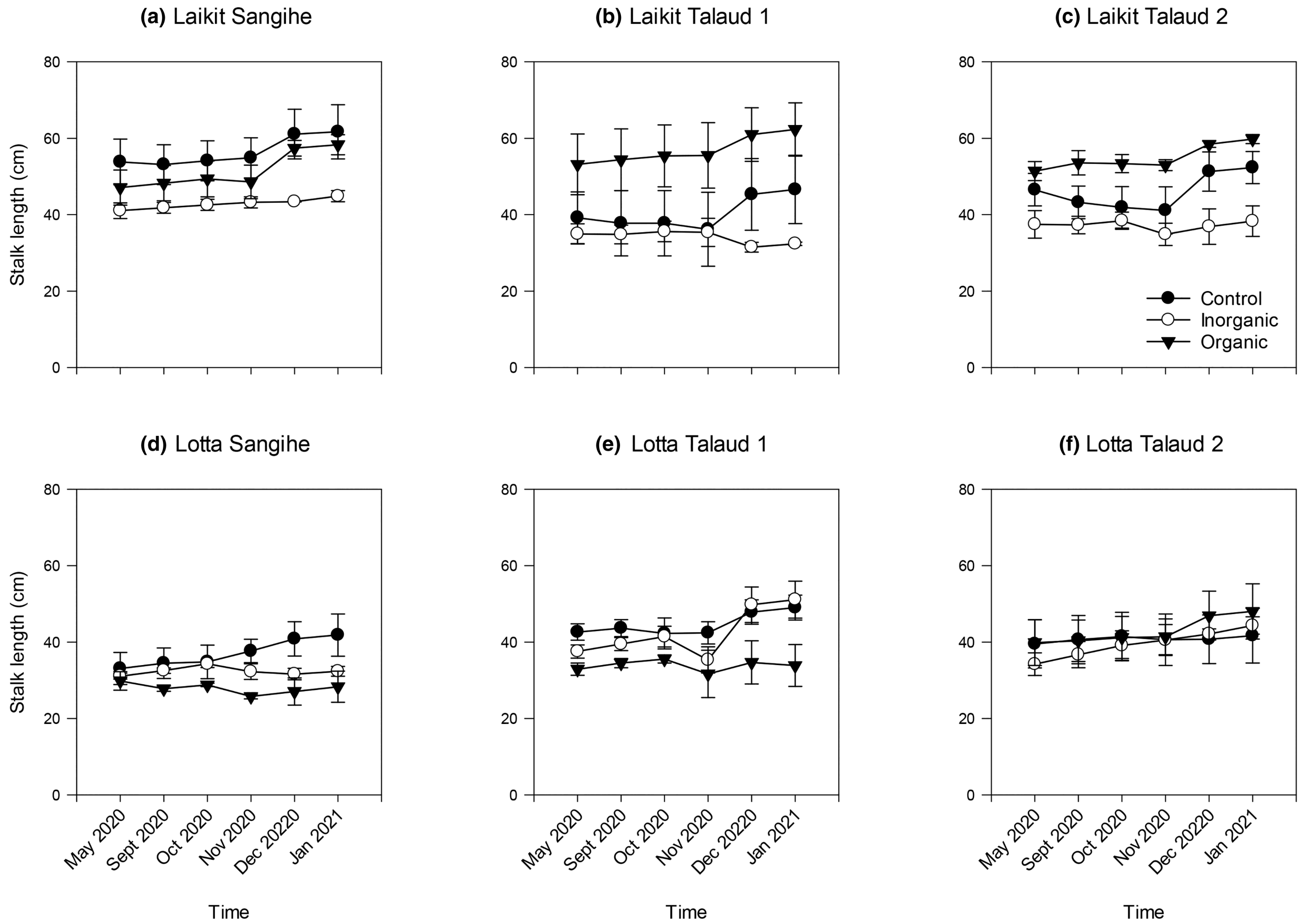

FIGURE 8 Data from the field trial on stalk length measured in response to site, fertiliser treatment and source material at six time points over the 12-month experiment in (a–c) the Laikit site and (d–f) the Lotta site for the source materials originating from (a, d) Sangihe, (b, e) Talaud 1, (c, f) Talaud 2. Means and SE are shown.

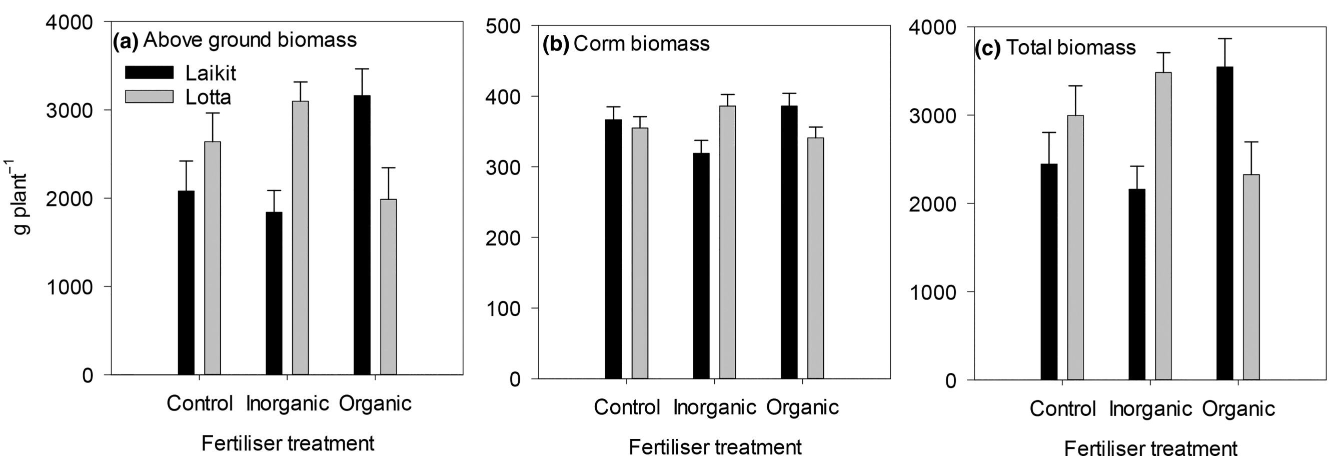

FIGURE 9 Final harvest data from the field trial showing the impact of the fertiliser treatment on (a) above-ground biomass, (b) corm biomass and (c) total biomass at the Laikit and Lotta field sites. Mean and SE of fresh biomass are shown.

substantial genetic variation in source material from North Sulawesi offering opportunities for extending cultivation trial to a greater range of sources material to ascertain potentially variation in yield as well as nutritional value.

Fertiliser application did not improve yield suggesting that the nutrient availability in control plots were sufficient to maintain plant growth and corm development for the duration of the experiment. This may be due to

TABLE 5 Statistics comparing differences in plant parameters linked to the treatments at the final harvest from the field trial at the two sites, Laikit and Lotta.

Parameter	Factor	df	*F*	*p*
Total Biomas$_{sLOG}$	Site	1, 54	0.41	0.524
	Source material	2, 54	1.54	0.223
	Fertiliser	2, 54	0.06	0.938
	Site × source material	2, 54	1.45	0.244
	Site × fertiliser	**2, 54**	**9.05**	**<0.001**
	Source material × fertiliser	4, 54	1.03	0.398
	Site × source material × fertiliser	4, 54	1.74	0.154
Corm biomass	Site	1, 54	0.07	0.798
	Source material	2, 54	2.27	0.113
	Fertiliser	2, 54	0.26	0.774
	Site × source material	2, 54	2.41	0.099
	Site × fertiliser	**2, 54**	**6.48**	**0.003**
	Source material × fertiliser	4, 54	1.02	0.406
	Site × source material × fertiliser	4, 54	2.14	0.089
Above-ground biomass$_{LOG}$	Site	1, 54	0.16	0.691
	Source material	2, 54	1.62	0.208
	Fertiliser	2, 54	0.09	0.918
	Site × source material	2, 54	2.29	0.331
	Site × fertiliser	**2, 54**	**8.63**	**<0.001**
	Source material × fertiliser	4, 54	1.24	0.305
	Site × source material × fertiliser	4, 54	1.97	0.113
Leaf length	**Site**	**1, 36**	**18.58**	**<0.001**
	Source material	2, 36	0.12	0.884
	Fertiliser	**2, 36**	**4.57**	**0.017**
	Site × source material	**2, 36**	**4.77**	**0.015**
	Site × fertiliser	**2, 36**	**8.35**	**0.001**
	Source material × fertiliser	4, 36	1.83	0.144
	Site × source material × fertiliser	4, 36	2.37	0.07
Leaf number$_{LOG}$	**Site**	**1, 36**	**168.16**	**<0.001**
	Source material	2, 36	1.07	0.354
	Fertiliser	**2, 36**	**5.89**	**0.006**
	Site × source material	2, 36	0.99	0.383
	Site × fertiliser	**2, 36**	**4.29**	**0.021**
	Source material × fertiliser	4, 36	1.57	0.203
	Site × source material × fertiliser	**4, 36**	**2.17**	**0.092**
Leaf width	**Site**	**1, 36**	**21.77**	**<0.001**
	Source material	2, 36	2	0.15
	Fertiliser	**2, 36**	**6.88**	**0.003**
	Site × source material	**2, 36**	**6.74**	**0.003**
	Site × fertiliser	**2, 36**	**10.59**	**<0.001**
	Source material × fertiliser	4, 36	1.7	0.171
	Site × source material × fertiliser	4, 36	2.45	0.064

(Continues)

TABLE 5 (Continued)

Parameter	Factor	df	*F*	*p*
Base length$_{LOG}$	**Site**	**1, 36**	**18.49**	**<0.001**
	Source material	2, 36	0.01	0.995
	Fertiliser	**2, 36**	**3.39**	**0.045**
	Site × source material	**2, 36**	**7.26**	**0.002**
	Site × fertiliser	**2, 36**	**10.6**	**<0.001**
	Source material × fertiliser	4, 36	2.19	0.089
	Site × source material × fertiliser	4, 36	2.05	0.109
Stalk length$_{LOG}$	**Site**	**1, 36**	**21.47**	**<0.001**
	Source material	2, 36	1.23	0.304
	Fertiliser	**2, 36**	**5.58**	**0.008**
	Site × source material	**2, 36**	**9.43**	**<0.001**
	Site × fertiliser	**2, 36**	**15.88**	**<0.001**
	Source material × fertiliser	4, 36	1.84	0.142
	Site × source material × fertiliser	**4, 36**	**2.76**	**0.042**
Stalk width$_{LOG}$	**Site**	**1, 36**	**16.12**	**<0.001**
	Source material	**2, 36**	**3.67**	**0.036**
	Fertiliser	**2, 36**	**6.85**	**0.003**
	Site × source material	**2, 36**	**3.33**	**0.047**
	Site × fertiliser	2, 36	2.32	0.113
	Source material × fertiliser	4, 36	1.02	0.411
	Site × source material × fertiliser	**4, 36**	**2.88**	**0.036**

Bold values indicate statistically significant effect.

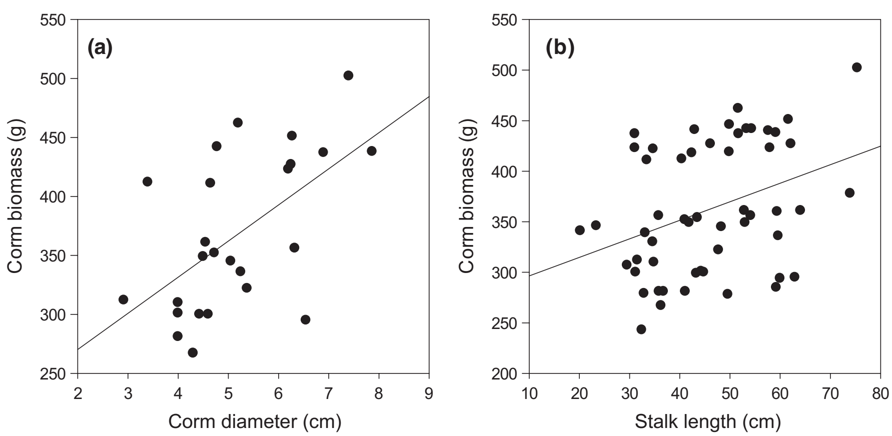

FIGURE 10 Relationship between (a) corm diameter and corm biomass and (b) stalk length and corm biomass based on the data from the final harvest at the two field trial sites Laikit and Lotta.

that the two sites used for cultivation, which prior to the trial had been used as fish ponds and pasture, currently supplied sufficient nutrients to maintain growth (Stoorvogel & Smaling, 1998). Further, it is also plausible that *C. merkusii* is adapted to low nutrient conditions wetland condition and hence did not require fertilisation. Clearly, there are direct environmental advantages as well as for farmers if fertilisation is not required, or that fertiliser requirements are low, for cultivation of *C. merkusii*. Currently fertilisers are subsidised for farmers to supply local food production on north Sulawesi and is hence often over applied (Islam & Beg, 2021; Warr & Yusuf, 2014). Indeed, over application of fertilisers severely impacts water quality with negative consequences for human health as well as for aquatic life. Further, application of nitrogen-rich fertilisers can dramatically increase N_2O emission from cultivated land particularly in waterlogged soils (Jovani-Sancho et al., 2022).

Corm Fe, Mn and K content were substantially higher at the Laikit (water-logged) site than the Lotta site despite lower content of these nutrients in the soil at the Laikit than Lotta site. This suggests that environmental factors

TABLE 6 Soil nutrient content (mg/kg) measured at the time of harvest at the two field trial sites; Laikit and Lotta.

Nutrient	Laikit	SE	Lotta	SE	SED	df	*F*-value	*p*-value
P	305	30	552	29	(42)	1, 34	34.72	<0.001
K	261	2	506	2	(34)	1, 34	51.58	<0.001
Mg	1130	150	2812	113	(187)	1, 34	80.57	<0.001
Mn	629	83	1343	175	(194)	1, 34	13.58	<0.001
Fe	23,610	1642	37,060	1241	(2058)	1, 34	42.73	<0.001
Cu	64.8	1.8	83.6	2.7	(3.3)	1, 34	32.4	<0.001

Note: Mean, SE and (SEDs) are shown as well as the degrees of freedom, *F* and *p*-values from the ANOVA.

TABLE 7 Leaf and corm nutrient content (mg/kg) measured at the time of harvest at the two field trial sites; Laikit and Lotta.

Nutrient	Laikit	Lotta	SED	df	*F*-value	*p*-value
Leaf						
P	3524	6022	757	1, 16	10.88	<0.005
K	38,540	47,220	4003	1, 16	4.7	<0.05
Mg	4350	6800	708	1, 16	11.99	<0.01
Mn	4946	1395	1374	1, 16	6.68	<0.05
Fe	482	237	102	1, 16	5.74	<0.05
Cu	20.2	22.2	2.9	1, 16	0.48	0.5
Corm						
P	522	1128	93	1, 16	42.69	<0.001
K	9980	5800	1832	1, 16	5.2	<0.05
Mg	445	515	48	1, 16	2.14	0.16
Mn	774	30	146	1, 16	25.78	<0.001
Fe	184	32	38	1, 16	16.26	<0.001
Cu	8.9	7.6	4.2	1, 16	0.1	0.75

Note: Mean and (SEDs) are shown as well as the degrees of freedom, *F* and *p*-values from the ANOVA. Nutrient analysis separated in relation to source material and fertiliser treatment are shown in Supplementary Information S1.

beyond soil nutrient content impact corm nutrient status. For example, the reducing soil conditions and low soil oxygen content under waterlogging may have impacted the uptake of nutrients, as well as the generally greater growth rates of the plants in the Laikit site. Iron uptake in plants is known to be influenced by valence, with reduced Fe^{2+} being far more readily absorbed than Fe^{3+} (Krohling et al., 2016). Irrespective of the physiological and biogeochemical processes (Chen et al., 1997; Fageria & Stone, 2006; Pezeshki et al., 1999; Szabonagy et al., 1994) behind these differences in corm nutrient status they clearly demonstrate that the site of cultivation (likely linked to water logging) directly impacts the nutrient status of the corm with implications for their values for human nutrition.

Our study suggests that *C. merkusii* has potential to be cultivated as a wetland crop building on the current traditional and more extensive use of *C. merkusii* historically (Englberger et al., 2008). This may offer improved security for local communities in areas that are becoming more exposed to variable environmental conditions including waterlogged conditions, which renders land unsuitable for many commonly grown crops as well as reducing reliance of rice imports in more remote island locations. Further, as *C. merkusii* is native to coastal areas in SE Asia its cultivation contributes to support of local practices and biodiversity (Rao et al., 2014). However, if *C. merkusii* is to become a more widely used crop following market development (Vinning, 2003) it is necessary to strengthen our understanding of its potential as a foodstuff as well as the best practices for its cultivation as a resilient sustainable crop suitable for both fresh water and coastal wetland conditions (Jackson, 2008).

The most important implication of our study in the context of developing environmentally sustainable agricultural practices is that it confirms *C. merkusii* has potential as a tropical crop that can grow well under waterlogged conditions in multiple soil types and with immediate utility for small holder farmers as an alternative food crop. This is a finding of great significance. While there is significant support among policy makers and researchers for paludiculture (wetland agriculture) in principle, studies of both temperate and tropical wetland agriculture crops as well as policy documents suggest that the identification of viable crops and routes for widespread adoption by farmers remain highly problematic (Dohong et al., 2018; Ward et al., 2020). Credible candidate wetland crops remain sparse (Uda et al., 2020) and those that have been identified tend to be biomass crops which would in many cases would require production on scales and via complex public-private financial models, which are likely to prove challenging to establish. This may be particularly the case in remote small holder communities in Indonesia. Equally such crops often require complex processing and marketing systems. Again, this may be challenging to deliver in remote tropical areas where resources may be limited. A crop which offers a more direct and relatively "low tech" adoption path by exchanging one food crop for another may have a better chance of being adopted in such areas. For this reason alone *C. merkusii* merits further exploration and may offer an excellent option in critically important environments in Indonesia. As such the plant may be of particular value in relation to the Indonesia government peatland restoration agency's current efforts to restore 2 million ha of drained and fire-prone peatlands (mainly in Kalimantan and Sumatra; Badan Restorasi Gambut, 2019). The success of these efforts is heavily dependent on providing alternatives to current land use patterns, which require drainage for successful crop production. Hence, crops that thrive in naturally waterlogged conditions are of potentially great value if they are to offer the prospect of alternative livelihoods for those currently living in areas that are targeted for rewetting. Our preliminary findings suggest that *C. merkusii* could play a part in a less damaging peatland cultivation system. In such areas *C. merkusii* production could potentially be grown on larger scales on rewetted peatlands alongside other restoration processes such are reforestation. However, in addition to the agronomic and nutritional data still needed to develop a successful new cropping system, further information on its use and market value and other social and economic barriers to adoption is needed (Vinning, 2003). Further information on the impacts of intensified *C. merkusii* cultivation on environmental conditions is also required. This may include questions related to the likely impact of the application of nitrogen-rich fertilisers on high N_2O emissions and of water table height on CH_4 effluxes in areas given over to *C. merkusii* cultivation (Griffis et al., 2020; Inubushi et al., 2003; Swails et al., 2021) and assessment of potential invasiveness. Measures to safeguard and ensure intact natural wetlands from increased commercial production of the crop may also need to be considered.

In conclusion, our research demonstrates that *C. merkusii* shows potential as a crop that can be cultivated successfully under waterlogged conditions without excessive additional fertilisation or land treatments or modifications. Despite being a wetland plant, it grows naturally in areas where water tables drop below 40 cm as well as under irrigated conditions at the dryland site. By being a wetland crop tolerant of periodic water table drops, *C. merkusii* offers a degree of resilient food production in situations where the water table varies. The potential for *C. merkusii* as a crop with regards to which source material is more productive and nutritional needs to be assessed over the full 3 year period it takes to produce full-sized corms. It is also imperative to investigate the environmental impact of cultivation of *C. merkusii* on biodiversity, water quality and greenhouse gas emissions. Further work on the social and economic costs and benefits of the crop is also required.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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