



Influence of weather and endogenous cycles on spatiotemporal yield variation in oil palm

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ABSTRACT

Oil palm is the major source of vegetable oil in the world and Indonesia is the main palm oil producing country. There is limited knowledge on the factors accounting for spatial and temporal variation in fresh fruit bunches (FFB) yield. Here we investigated relationships between weather and endogenous factors with FFB yield and its components (bunch number and individual bunch weight) using data collected from well-managed plantations in Indonesia. The database included many sites and years (total of 136 block-years observations), portraying a wide range of FFB yield and environmental conditions. We used average annual values to detect spatial variations in yield associated with weather, and monthly values to detect temporal yield variations in yield associated with weather and endogenous cycles. We found that water stress was the key factor accounting for the spatial and/or temporal variation in FFB yield. Our analysis also highlights the importance of vapor pressure deficit (VPD) as a stress factor in oil palm, with this study being the first to demonstrate the negative relationship between yield and VPD and yield and water-use efficiency at the block level. Meteorological anomalies during the bunch failure, anthesis, and sex differentiation periods had the largest impact on yield. Besides climate factors, we confirmed the existence of endogenous yield cycles, with high-yield cycles typically followed by low-yield cycles and *vice versa*. Our findings extend current knowledge about sources of variation in oil palm yield, providing useful information to describe oil palm production environments and improve oil palm modeling and yield forecasting.

1. Introduction

Oil palm is the major source of vegetable oil in the world. Indonesia is the main oil palm producing country, currently producing this crop in ca. 14.7 million hectares and accounting for 60% of global production (FAOSTAT, 2020). The fresh fruit bunches (FFB) are collected every

7–15 days and sent to the mill to extract the oil, which is used for a wide array of products, including food, cosmetics, and biodiesel. Previous studies assessing relationships between FFB yield and meteorological factors can be grouped into three categories. The first category includes regional studies based on coarse, aggregated annual FFB and weather data that aim to generate predictive models for yield forecasting and for

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land suitability evaluation of oil palm (Foong Weng Sum and Shukor, 2019; Hashemvand Khiabani and Takeuchi, 2020; Oettli et al., 2018; Rhebergen et al., 2016). The second category includes local studies looking at associations between FFB yield and weather variables based on data collected from a small number of sites and/or years (Ambar Suharyanti et al., 2020; Brum et al., 2021; Caliman, 1992; Cock et al., 2016; Combres et al., 2013; Dufour et al., 1988; Meijide et al., 2017; Rhebergen et al., 2019; Sidhu et al., 2021; Stiegler et al., 2019; Yong Keong and Wong Keng, 2012). Finally, the third category include ecophysiological studies at process level, and simulation models testing internal consistency of the presumed mechanisms (Henson, 2007, 2000; Perez et al., 2018a, 2018b; Van Kraalingen et al., 1989). A major limitation of these previous studies is the narrow range of soil and weather environments that were explored which limits the extrapolation of results to other conditions. Furthermore, poor agronomic management may constrain the ability to find relationships between FFB yield and meteorological factors, as reported FFB yields are typically well below the 30 to 40 t FFB ha⁻¹ range that are achieved in well-managed plantations (Monzon et al., 2021). Finally, previous studies have not investigated how these factors affect the yield components, namely, bunch number (BN) and individual bunch weight (BW). We are not aware of any previous studies that have explicitly used field-level yield data collected from well-managed plantations across a wide range of environments to investigate the association of weather factors with FFB yield and its components.

Another limitation from previous studies is the use of short time series to assess the influence of weather on FFB yield. In contrast to annual crops, oil palm FFB yield is determined over a long period of time, taking approximately 39 months from the initiation of a bunch primordia to harvest (Breure and Menendez, 1990). Previous studies have identified three main critical stages for yield determination, including bunch failure (5 to 6 months before harvest), inflorescence abortion (10 to 12 months before harvest), and sex determination (24 to 28 months before harvest) (Adam et al., 2011; Breure and Menendez, 1990; Carr, 2011; Combres et al., 2013). Thus, yield at any one time would be expected to be associated with the weather patterns over the previous three years.

Empirical evidence suggest that FFB yield is also associated with endogenous yield cycles, that is, alternate cycles of high and low productivity that are independent of environmental conditions (Breure and Corley, 1992; Corley and Breure, 1992). Breure and Corley (1992) showed that fruiting activity (defined as the total bunch weight or bunch number at given point of time, including both ripe and unripe bunches) affects inflorescence abortion and individual bunch weight (BW), leading to cycles of high (low) productivity being followed by cycles with low (high) productivity. Hence, the analysis of temporal variations in FFB yield requires long-term data that takes into account endogenous yield cycles.

The influence of vapor pressure deficit (VPD) on crops has largely been documented with reference to water use efficiency (WUE), defined here as the economic yield produced per unit of evapotranspiration (Abbate et al., 2004; Kemanian et al., 2005; Tanner and Sinclair, 1983). In most crops, *ceteris paribus*, as VPD increases, transpiration increases and water use efficiency decreases. In tropical crops such as oil palm and cassava, stomata partially close in response to increased VPD above a threshold level (Dufrene and Saugier, 1993; Cock and Connor, 2021). The partial closure of stomata not only reduces transpiration but also reduces photosynthesis. The possible negative effects of partial stomatal closure on photosynthesis and how this might influences yield has been pointed out (Henson, 2007, 2000; Smith, 1989). However, we are not aware of any study that has assessed the influence of VPD on oil palm FFB yields using block-level data. Indeed, while current simulation models for oil palm include a potential evapotranspiration routine to estimate the water balance, they have not been evaluated on their capacity to reproduce the direct effect of VPD on photosynthesis and WUE (Hoffmann et al., 2014; Huth et al., 2014). The partial closure of stomata

in response to increased VPD is likely to be advantageous in conditions when soil water availability is limited; however, when there is abundant readily available soil water, the partial closure of stomata may be detrimental to yield (Cock and Connor, 2021). Hence, we surmised that it would be useful to study the relationship between FFB yield and VPD to identify production environments that, given the same water availability, have a different attainable FFB yield level due to contrasting VPD regimes, and, furthermore, to improve prediction of FFB yield using empirical and process-based crop models.

A rigorous evaluation of the influence of environmental variables on spatial and temporal variation in oil palm FFB yield and its components is missing. To fill this knowledge gap, we used a novel database including long-term yield records from well-managed plantations located across a wide range of environments in Indonesia. The goal was to establish relationships between FFB yield, WUE, and meteorological factors and understand endogenous yield cycles. Implications for oil palm agronomists and crop modelers are discussed.

2. Materials and methods

2.1. Database from well-managed plantations

We made an explicit effort to collect data from blocks with an excellent agronomic background so that one can assume that the observed FFB yield variation was driven by climate and endogenous cycles rather than management practices. On request, five major commercial oil palm companies provided data from their highest-yield blocks located in mineral soils across Indonesia's main oil palm producing areas. Selected blocks were rainfed and had good drainage, no flood risk, and no presence of water table. These companies provided FFB yield data on a monthly basis from 14 well-managed blocks across the country (Fig. 1). Agronomists from each company indicated that selected blocks received periodic fertilizer to minimize nutrient limitations and, whenever necessary, selective pesticide applications to avoid yield losses due to diseases, weeds, and insect pests. As a result, FFB yield in the selected blocks was consistently higher than that in other blocks located in the same regions. While we are not allowed to disclose the exact location of these blocks, we provide their approximate geographic location in Fig. 1 as well as the associated management and biophysical background (Tables 1 and 2).

Data were screened for missing and erroneous entries. Similarly, we excluded FFB yield data from the initial eight years after establishment to avoid the confounding effect associated with the steep yield increase that occurs in early years (Hoffmann et al., 2014). On average, there were 10 years of monthly FFB yield, BW, and BN data available for each block (total of 136 block-year observations). Blocks were planted with dura x pisifera (DxP) hybrids selected for broad adaptation. Palm density ranged from 129 to 143 palms ha⁻¹ across these blocks. These values are within the optimal range reported for oil palm, and there was no need to correct FFB yield data based on differences in palm density (Corley and Tinker, 2015; Corley, 1973). For data description purposes, we grouped the 14 blocks into four regions based on their proximity and similarity in annual weather patterns: Northern Sumatra (NS), which includes North Sumatra and Riau provinces, Southern Sumatra (SS), which includes South Sumatra and Lampung provinces, Central Kalimantan (CK), and Eastern Kalimantan (EK). Our database portrayed well the spatial distribution of the oil palm area in Indonesia and the associated weather and soil variation (Fig. 1; Tables 1-2).

2.2. Weather data and calculation of water stress index

Measured daily weather data (sunshine hours, minimum and maximum temperature, relative humidity, and wind speed) from the nearest meteorological station to each block were retrieved from the Indonesian Meteorological, Climatological, and Geophysical Agency (BMKG; <http://www.bmkg.go.id/>) (Fig. 1 and Table 1). Weather data

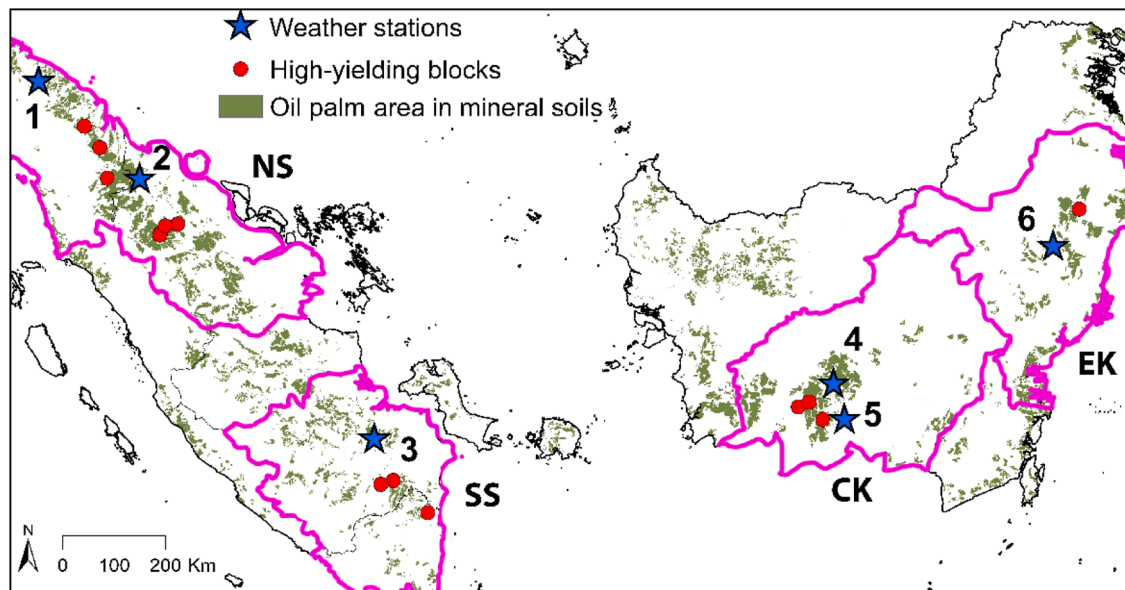


Fig. 1. Location of the 14 well-managed blocks (red circles) and associated weather stations (blue stars) used in our study to assess the influence of weather and endogenous cycles on oil palm FFB yield in Indonesia. Weather station names and codes are shown in Table 1. Oil palm area in mineral soils is shown in green. Also shown are the four regions delineated for our study: Northern Sumatra (NS), Southern Sumatra (SS), Central Kalimantan (CK), and Eastern Kalimantan (EK).

Table 1

Number of blocks, average plant age (and associated range), time period with available data, weather stations (and associated codes shown in Fig. 1), and dominant soil texture and associated plant available water holding capacity within the rootable soil depth (TAW, 0–1 m soil) for the four regions in Indonesia included in our analysis.

Region (and number of blocks)	Palm age	Years	Weather stations (and codes)	Soil texture (and TAW in mm) [†]
Northern Sumatra (<i>n</i> = 7)	17 (9–24)	2002–2018	Tuntungan (1), Bagansinemba (2)	Sandy clay loam (89), sandy clay (114), sandy loam (147)
Southern Sumatra (<i>n</i> = 3)	17 (10–28)	2004–2018	Palembang (3)	Sandy clay loam (89)
Central Kalimantan (<i>n</i> = 3)	22 (10–30)	2005–2018	Parenggean (4), Sampit (5)	Clay loam (137), sandy clay loam (89), sandy loam (147)
Eastern Kalimantan (<i>n</i> = 1)	25 (19–30)	2004–2015	Muara Ancalong (6)	Silty clay loam (158)

[†] TAW for each textural class was estimated using the pedo-transference functions for tropical soils developed by Hodnett and Tomasella (2002).

Table 2

Annual means for key meteorological variables for each region, including average incident radiation, maximum and minimum temperature (Tmax and Tmin), mean vapor pressure deficit (VPD), total grass-based reference evapotranspiration (ET_o), and total precipitation. Parenthetic values indicate ranges across block-years for each region.

Region	Radiation ^a (MJ m ⁻² d ⁻¹)	Tmax (°C)	Tmin (°C)	VPD (kPa)	ET _o ^b (mm)	Precipitation (mm)
Northern Sumatra	17.2 (14.8–18.5)	28.7 (27.7–29.2)	24.1 (23.8–24.5)	0.43 (0.37–0.68)	1274 (1151–1346)	2011 (983–3915)
Southern Sumatra	16.5 (16.0–17.3)	32.4 (31.8–32.9)	23.7 (23.5–24.2)	0.67 (0.60–0.76)	1377 (1317–1437)	2545 (1835–3642)
Central Kalimantan	16.6 (15.4–17.5)	31.9 (31.0–33.3)	23.0 (22.4–23.4)	0.63 (0.54–0.70)	1355 (1308–1419)	2582 (1660–4613)
Eastern Kalimantan	16.3 (15.0–17.7)	28.5 (28.0–29.0)	23.2 (23.0–23.4)	0.29 (0.25–0.33)	1164 (1087–1251)	2794 (2106–3701)
All block-years	16.8 (14.8–18.5)	30.1 (27.7–33.3)	23.7 (22.4–24.5)	0.51 (0.25–0.76)	1303 (1087–1437)	2311 (983–4613)

^a Radiation was derived from sunshine hours following the Angstrom equation.

^b ET_o was calculated from climate data using the Penman-Monteith equation.

was quality controlled and gaps were filled based on correlations between the target station and one to three adjacent weather stations following the methodology described by van Wart et al. (2013) and references cited therein. The number of corrected and/or filled data was always lower than 3% for all variables. When data gaps persisted after the use of adjacent weather stations, missing values were filled by NASA-POWER gridded weather (NASA LaRC POWER Project, 2021) after calibration with the measured BMKG weather data. On-site monthly precipitation data was available for each block; daily values were generated based on the occurrence of wet days and daily amounts reported by the nearest BMKG meteorological station. Following Allen et al. (1998), sunshine hours were converted into incident solar radiation using the Angstrom equation while daily mean vapor pressure deficit (VPD) was estimated based on temperature and relative humidity.

We followed the FAO-56 crop coefficient method to estimate the crop evapotranspiration using crop specific coefficients and a daily water balance (Allen et al., 1998). The method consists of three steps:

- 1 The grass-based reference evapotranspiration (ET_o) is calculated from climate data using the Penman-Monteith equation.
- 2 The non-water limited crop evapotranspiration (ET_c) is calculated based on ET_o, after adjustment for oil palm:

$$ET_c = K_c * ET_o \quad (1)$$

where K_c is a crop-specific coefficient and set at one in the case of oil palm (Carr, 2011). Hence, in the case of oil palm, E_{Tc} is equal to E_{To} .

- 3 In water-limited conditions, the actual crop evapotranspiration (E_{Ta}) is calculated based on E_{To} after adjustment by a reduction factor to account for the effect of soil water limitation:

$$E_{Ta} = K_s * E_{To} \quad (2)$$

where K_s is a reduction factor ranging from zero to one and estimated as follows:

$$K_s = (TAW - Dr_i) / (TAW - RAW) \quad (3)$$

where TAW is the plant available water within the rootable soil depth (i.e., water stored in the root zone between field capacity and permanent wilting point, Table 1), Dr_i (mm) is the rootzone depletion, and RAW (mm) is the readily available water (i.e., a fraction of TAW below which the crop starts to suffer water stress). For mature oil palm, this fraction is about 0.65 (Allen et al., 1998). For our study, we set rootable soil depth at 1 m because most oil palm roots do not exceed this depth (Nelson et al., 2006) and considering that no restrictive soil layer within the upper meter was reported for any of the 14 blocks included in our database.

To determine Dr_i , we used a daily water balance based on a simple tipping bucket approach:

$$Dr_i = Dr_{i-1} - P_i + E_{Ta_i} + DP_i \quad (4)$$

where Dr_i (mm) is the root zone depletion at the end of day i , Dr_{i-1} (mm) is the root zone depletion at the end of the previous day $i - 1$, P_i (mm) is the precipitation on day i , E_{Ta_i} (mm) is the actual crop evapotranspiration on day i and DP_i (mm) is the water loss out of the root zone by deep percolation on day i . We assumed there was no run-off as the land was relatively flat, and with a permanent vegetation ground cover to minimize run-off and erosion. In turn, deep percolation (DP) was calculated as follows:

$$DP_i = P_i - E_{Tc_i} - Dr_{i-1} \quad (5)$$

Finally, the degree of water limitation was calculated as:

$$WSI = 1 - (E_{Ta} / E_{Tc}) \quad (6)$$

where WSI is water stress index, which can range from 0 (no stress) to 1 (maximum stress).

2.3. Relationships between yield, water-use efficiency, and meteorological factors

We used average annual values to investigate spatial variation in FFB yield and WUE associated with weather, while we computed monthly values to assess temporal variation in yield associated with weather and endogenous cycles. Spatial variation in oil palm productivity was explored by analyzing relationships between average annual FFB yield (and its component) at each site with a series of weather factors, including radiation, temperature, VPD, E_{To} , precipitation, and WSI. A similar approach was followed to investigate the association between WUE and VPD. In our study, WUE was estimated as the ratio between annual FFB yield and E_{Ta} .

Assessing temporal FFB yield variation in oil palm is difficult due to: (i) the long period of yield determination, with ca. 39 months from bunch initiation to harvest (Breure and Menendez, 1990); (ii) differences in yield level across sites due to climate, soil, and management factors; and (iii) age-related trends in yield and yield components. To avoid these confounding factors, we detrended the data and we looked at the relationship between monthly FFB yield anomalies and detrended

monthly weather anomalies computed for each of the previous 40 months. We followed a three-step approach to estimate monthly yield anomalies. First, we fitted a linear model to the relationship between annual FFB yield and plantation age and used it to detrend the annual FFB yields for each block. Subsequently the monthly yield anomalies were calculated as follows:

$$Ya_{ijk} = (x_{ijk} - x_{ij}) / x_{ij} \quad (7)$$

where Ya is the yield anomaly in month i , in block j , and year k and x is the detrended yield. The resulting yield anomalies estimated following Eq. (7) were expressed as percentage of the average yield at each block (x_{ij}) to remove any site-effect on FFB yield associated with the agronomic and biophysical background. A similar approach was followed to estimate anomalies for monthly values of BW, BN, and meteorological variables. For the analysis of temporal variation, meteorological variables were computed on a monthly basis. We used Pearson correlation to investigate associations between FFB yield (and yield components) anomalies in month i versus anomalies in meteorological variables calculated separately for each of the previous 40 months (i.e., from $i-1$ to $i-40$). Correlation among anomalies in monthly meteorological variables was low ($r < 0.50$). We used heat maps to visualize the strength and sign of the association between yield and weather anomalies.

2.4. Endogenous FFB yield cycle analysis

We further investigated temporal variation in FFB yield by assessing FFB yield cycles over time and associated drivers in terms of yield components (BN and BW), separately on an annual and monthly basis. For the analysis based on annual values, we calculated annual anomalies in FFB yield and yield components based on the relationship between annual FFB yield and age for each block and expressing the residuals as percentage of the average FFB yield in each block. A similar approach was followed to estimate annual anomalies for BW and BN.

For the analysis based on monthly values, we followed the same approach explained in Section 2.3 to detrend monthly yield values. Using the detrended data, we estimated the “fruiting activity”, defined as the number of fruit bunches developing at any one time. The fruiting activity may have large effects on future bunch number and mean bunch weight. To estimate fruiting activity in a given month we followed the approach described by Corley and Breure (1992):

$$FA_i = 0.41 * BN_{i+1} + 0.32 * BN_{i+2} + 0.23 * BN_{i+3} + 0.14 * BN_{i+4} + 0.05 * BN_{i+5} \quad (8)$$

where FA_i is the fruiting activity in month i and BN_i is the monthly BN after being detrended for age and block effect in month i . For both analysis (i.e., based on annual or monthly scales), we used Pearson correlation to assess the strength of the association between yield (and its components) anomalies in year k (or month i) versus FFB yield anomalies in subsequent years (or months).

3. Results

3.1. Variation in FFB yield and yield components

The average annual yield across all block-years was 31.3 t FFB ha⁻¹, the spatial variation in FFB yield was not pronounced (CV = 10%), with highest and lowest FFB yields in EK and SS, respectively (Table 3). We note that the relatively low FFB yield in SS (ca. 26 t ha⁻¹) was attributed to water limitation and not poor management. Temporal variation in FFB yield (quantified using inter-annual CV) was similar, averaging 12% across the 14 blocks (range: 7 to 22%). In relation to yield components, BN averaged 1437 ha⁻¹, ranging from 694 to 2980 ha⁻¹ across block-years (CV = 27%). In contrast, BW did not vary as much as BN, ranging from 12 to 31 kg bunch⁻¹ (CV = 17%), averaging 23 kg bunch⁻¹ across block-years (Table 3). BN was negatively correlated with palm

Table 3

Average annual fresh fruit bunch (FFB) yield, bunch number (BN), and individual bunch weight (BW) for each of the four regions considered in our study. Parenthetic values indicate ranges across block-years for each region. In all cases, annual FFB yields were based on a calendar-year basis (*i.e.*, from Jan 1 to Dec 31).

Region	Annual FFB yield (t ha ⁻¹)	BN (ha ⁻¹)	BW (kg)
Northern Sumatra	32.7 (26.3–41.6)	1534 (1032–2980)	22.0 (12.2–30.5)
Southern Sumatra	26.0 (18.2–35.8)	1085 (694–1700)	24.8 (18.2–30.4)
Central Kalimantan	32.3 (26.6–38.6)	1446 (1087–2252)	22.9 (13.0–28.5)
Eastern Kalimantan	34.6 (27.1–38.3)	1729 (1281–2782)	20.9 (13.2–25.8)
All block-years	31.3 (18.2–41.6)	1437 (694–2980)	22.7 (12.2–30.5)

age (–118 bunches ha⁻¹ y⁻¹) until an age of 15 years, followed by a slower decline onwards (–6 bunches ha⁻¹ y⁻¹). In contrast, BW was positively correlated with palm age, with a sharp increase (+1 kg y⁻¹) up to a palm age of 16 years, followed by a gradual increase onwards (+0.2 kg y⁻¹) (**Supplementary Fig. S1**).

We investigated the portion of FFB yield variation that was accounted for by each of the yield components (BN and BW). A linear-plateau function provided the best fit to the relationship between FFB yield and BN ($p < 0.01$), accounting for 61% of the observed FFB yield variation (**Fig. 2**). In contrast, there was a weak relationship between FFB yield and BW ($p = 0.06$, $r^2 = 0.03$, **Fig. 2a**, inset). The FFB yield increased linearly with BN up to 1410 bunches ha⁻¹ (or 10 bunches per palm y⁻¹). Above that threshold, there was no further increase in FFB yield with increasing BN. Finally, there was a negative association between BW and BN ($r^2 = 0.67$, $p < 0.01$, **Fig. 2b**).

Monthly variation in FFB yield and yield components differed across the four regions (**Fig. 3**). For example, FFB yield peaked in January (EK), May–July (CK), August (NS) and November (SS), with lowest FFB yields occurring in February (NS and SS), June (EK), and December (CK). Similar trends were observed for BN (**Fig. 3b**). Variation in BW across months was smaller than for BN (average CVs = 3 versus 17%) (**Fig. 3c**).

3.2. Drivers of spatial variation in FFB yield and water-use efficiency

The greatest spatial variation of meteorological variables was for VPD (CV = 35%) and precipitation (CV = 17%) (**Table 2**). Annual precipitation averaged 2311 mm, ranging from 2011 (NS) to 2794 mm (EK). Average VPD was 0.51 kPa, ranging from 0.29 (EK) to 0.69 kPa (SS). In contrast, temperature (CV = 4%) and radiation (CV = 2%) were relatively stable across sites. Similarly, the range in annual ETo was relatively narrow, from 1164 (EK) to 1377 mm (SS), with an average CV of 7% (**Table 2**).

Precipitation varied among months (average CV = 18%) but the degree of variation depended upon region. The most uniform distribution across the year was NS and the least SS (**Fig. 4a**). In SS, 75% of the total precipitation fell from November to April. In contrast with precipitation, ETo varied little between months with average CVs of 6% (**Fig. 4b**). Across regions, the WSI was greatest in SS, especially during July–October, due to a combination of low and ill-distributed precipitation, and slightly higher ETo than in other regions (**Fig. 4c**). In contrast, there was no water deficit in EK due to high and well-distributed precipitation and comparably lower ETo than at other sites. WSI was intermediate in NS and CK.

We did not detect significant associations between annual FFB yield and annual precipitation ($p = 0.33$, $r^2 = 0.08$) (**Fig. 5a**). Yield was negatively correlated with both VPD and WSI ($p < 0.05$, **Fig. 5b** and **5c**). However, the VPD and WSI effects were confounded as the location with highest VPD (South Sumatra) also exhibited the highest WSI. As a result, we could not conclusively determine a direct relationship between FFB yield and VPD. In contrast, a linear-plateau model portrayed well the relationship between annual FFB yield and WSI (**Fig. 5c**). Annual FFB yield remained unchanged with WSI lower than 0.08 but then dropped linearly with increasing WSI at a rate of 1.4 t ha⁻¹ FFB per 0.01 change in WSI. Relationships between FFB yield with temperature and solar radiation were not statistically significant or were confounded due to co-

variation with other meteorological factors. Finally, yield components were unrelated with meteorological variables, except for a positive relationship between BN and incident solar radiation and a negative association between BN and VPD ($p < 0.05$) (**Supplementary Figures S2–S3**).

Annual WUE was estimated as the ratio between annual FFB yield and ETo. Across sites, WUE averaged 26 kg FFB ha⁻¹ mm⁻¹, ranging from 23 (SS) to 30 kg FFB ha⁻¹ mm⁻¹ (EK). There was a strong association between WUE and VPD variation across sites, accounting for 70% of the observed variation (**Fig. 6**).

3.3. Temporal variation associated with meteorological variables

Despite the inherent noise in the data because of pooling data from different plantations, our detrending method allowed us to identify relationships between monthly FFB yield anomalies and fluctuation in

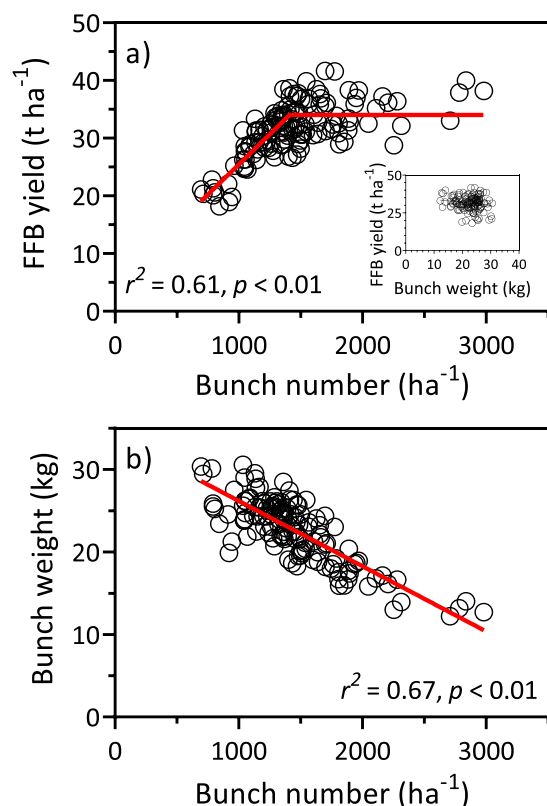


Fig. 2. Annual oil palm fresh fruit bunch (FFB) yield and yield components in well-managed blocks. (a) Relationship between FFB yield and bunch number, inset shows the relationship between FFB yield and bunch weight. (b) Relationship between bunch weight and bunch number. Fitted linear models (red solid lines) and coefficient of determination (r^2) are shown. Data are block-year observations ($n = 136$). Fitted regression lines do not imply causality; instead, they are shown to illustrate that the two variables in each plot are not independent in the sense that one variable does provide information about the other variable.

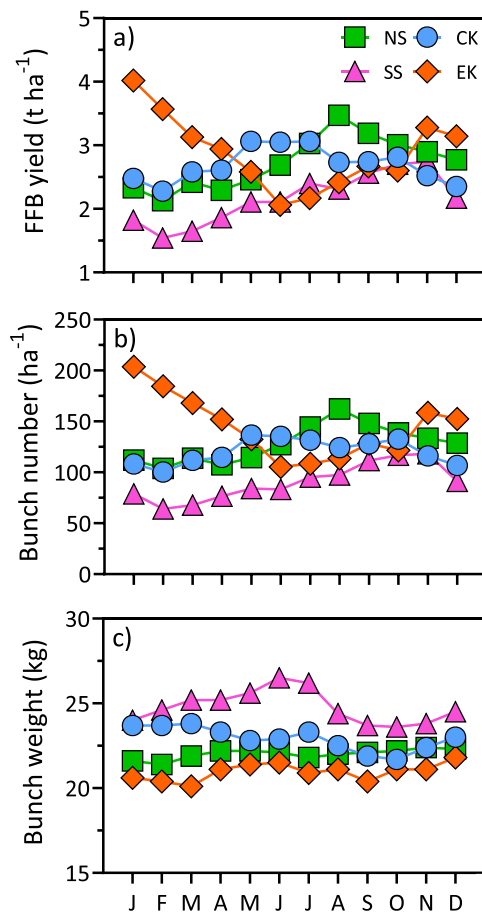


Fig. 3. Average monthly fresh fruit bunch (FFB) yield (a), bunch number (b), and bunch weight (c) for the four regions: Northern Sumatra (NS), Southern Sumatra (SS), Central Kalimantan (CK) and Eastern Kalimantan (EK). Data are averages for all blocks within a region.

temperature, VPD, and WSI during specific crop stages (Fig. 7). For example, higher mean temperature and VPD between 1 and 5 months before harvest has a negative effect on FFB yield due to lower BW. Similarly, FFB yield was negatively associated with WSI and VPD during inflorescence abortion and sex differentiation stages, driven by changes in BN and, to a lesser extent, BW. Surprisingly, we found that higher VPD and WSI 12 to 18 months before harvest have a positive effect on FFB yield due to higher BN.

The FA was not affecting our analysis of meteorological variables, because we found no correlation between anomalies in weather variables *versus* those in FA ($r < 0.07$, $p > 0.05$).

3.4. Temporal variation associated to yield cycles in oil palm

There was a negative association between annual FFB yield in year k with the FFB yield in years $k + 1$ and $k + 2$ (Table 4). In other words, years with above-average yields were followed by years with below-average yields and *vice versa*. This trade-off was more pronounced when comparing a given year k *versus* year $k + 2$ due to the combined negative effect on BN and BW. In contrast, the trade-off between consecutive years was driven only by BN, with a positive effect on BW that was not enough to offset the reduced BN. We did not observe any statistically significant correlation among yields from year $k + 4$ onwards ($p > 0.44$).

The analysis based on monthly anomalies allowed us to identify more precisely the drivers for the relationships found using annual FFB yields (Fig. 8). We found that current fruiting activity had a negative

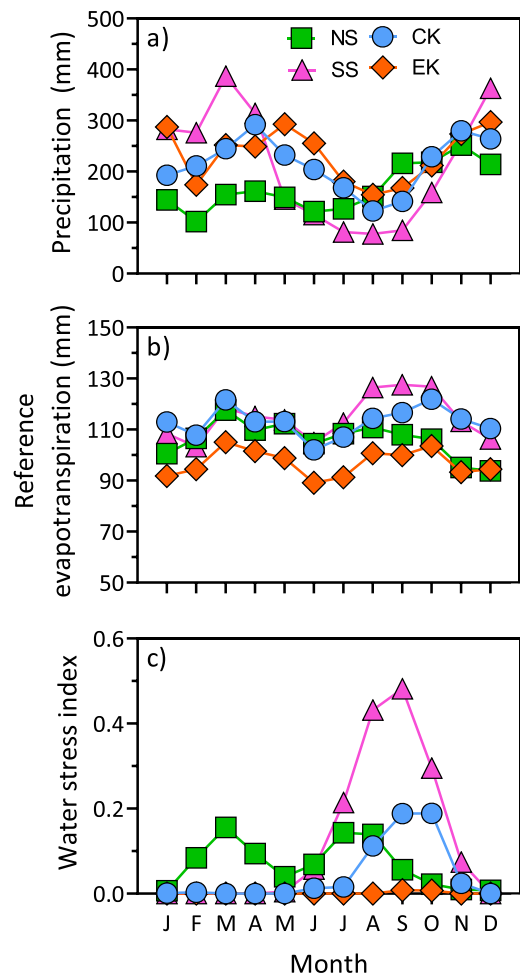


Fig. 4. Annual patterns in (a) monthly precipitation, (b) reference evapotranspiration (ETo), and (c) water stress index for the four regions: Northern Sumatra (NS), Southern Sumatra (SS), Central Kalimantan (CK), and Eastern Kalimantan (EK). Data are averages for all blocks within a region. Description of the methodology used to estimate ETo and water stress index is provided in Section 2.2.

impact on future FFB yield and this effect was driven by a negative effect on BN during bunch failure and anthesis (3–7 months after harvest) and sex differentiation stages (22–25 months after harvest). In contrast, current fruiting activity had a positive impact on BW around 14–18 months after harvest, which coincides with the stages when the number of flowers per spikelet and frame weight are determined, leading to slightly higher FFB yields.

4. Discussion

Average yield across all block-years of 31.3 t FFB ha⁻¹ was 75% higher than average national FFB yield in Indonesia (18 t ha⁻¹) and was comparable to the attainable yield estimated using process-based crop models in previous studies (31.6 t FFB ha⁻¹, Monzon et al., 2021). Hence, the high yields achieved in these blocks and the similarity to the estimated attainable yield gives confidence that spatial and temporal variation in FFB yield in our database was mostly associated with weather, soil, and endogenous yield cycles rather than agronomic management. We acknowledge that our range of weather and soils may not fully capture the range of biophysical environments where oil palm is grown around the world. While our range of environmental conditions may be missing severe water-limited environments, such as those in Sub-Saharan Africa, we note that our range is highly representative of

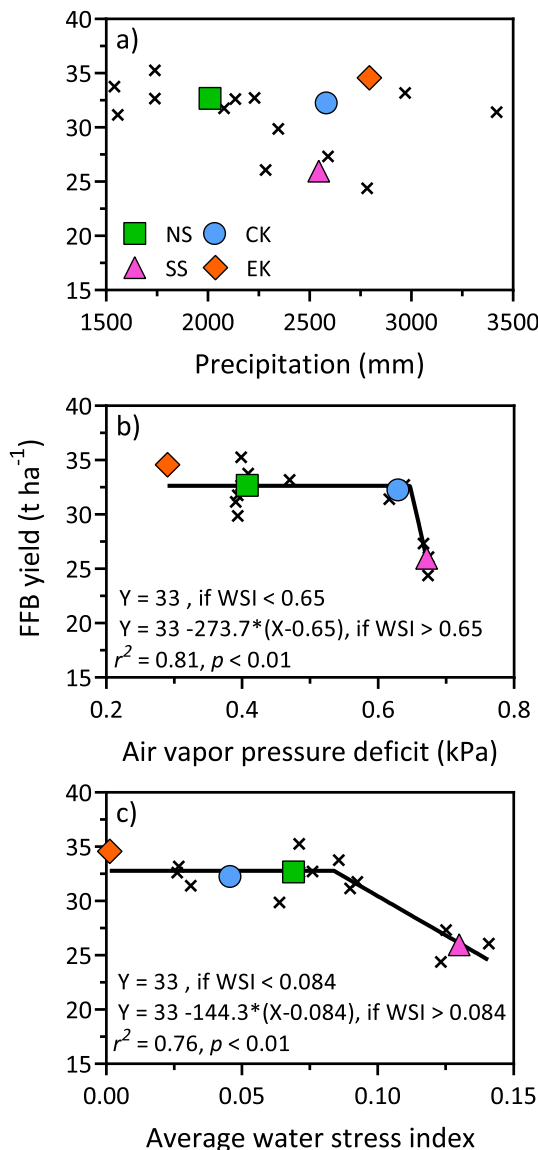


Fig. 5. Annual fresh fruit bunch (FFB) yield as a function of annual: (a) precipitation, (b) air vapor pressure deficit, and (c) average water stress index. In all cases, annual FFB yields were based on a calendar-year basis (i.e., from Jan 1 to Dec 31). Relationships between variables are shown when statistically significant and are based on the pooled data from the individual blocks ($n = 14$), which are shown with crosses. Data are the average for each block across year, also shown are average values for each region: Central Kalimantan (CK), Eastern Kalimantan (EK), Northern Sumatra (NS), and Southern Sumatra (SS).

the environments where most oil palm production takes place, including Indonesia and Malaysia, which together account for nearly 75% of global crude oil palm output (FAOSTAT, 2020).

We acknowledge that our analysis cannot completely dissect the individual contribution of weather and endogenous yield cycles to the overall temporal variation in FFB yield. However, one can assume that FA was not affecting our analysis of weather factors and *vice versa*, considering that the correlations between detrended meteorological variables and detrended FA were weak and not statistically significant ($p > 0.05$). The main meteorological factors influencing yields of oil palm have traditionally been taken as temperature, precipitation, and solar radiation (Corley and Tinker, 2015). Here, we found that the relationship between precipitation and FFB yield, despite a wide range from 1540 mm to more than 3420 mm, was loose and not significant whereas

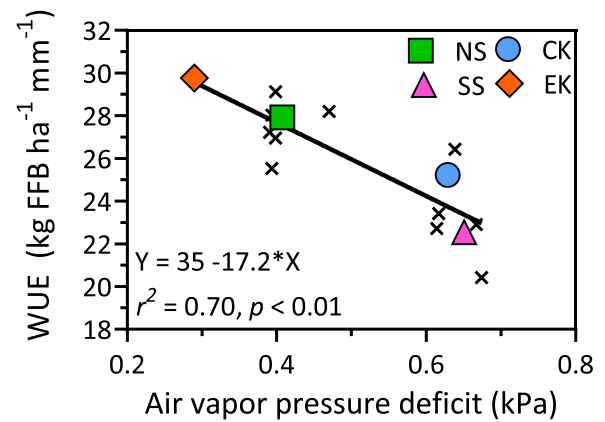


Fig. 6. Relationship between water-use efficiency (WUE) and daily mean air vapor pressure deficit. The model was fitted using the pooled block data ($n = 14$). Data are the average for each block across years, also shown are average values for each region: Central Kalimantan (CK), Eastern Kalimantan (EK), Northern Sumatra (NS), and Southern Sumatra (SS).

FFB yield was closely associated with WSI (Fig. 5 and 7). The lack of a close association of FFB yield with precipitation coupled with the close association with WSI indicates that WSI, which is based on a water balance and considers differences in ETo and soil water storage across sites as well as seasonal variation in water availability, is a better predictor of water limitation than the empirical rules (e.g., number of months with less than 100 mm) to characterize production environments as done in most previous studies (Paramanathan, 2003; Rhebergen et al., 2016). This appraisal is in accordance with the effective use of water balance model rather than simply precipitation to analyze weather effects on yield over prolonged periods (Cock et al., 2016; Sidhu et al., 2021; Surre, 1968).

Characterizations of the optimal conditions for oil palm growth include air humidity of more than 85% (Carr, 2011). Smith (1989) assessed the effects of VPD on stomatal behavior and photosynthetic rate in oil palm under various conditions of soil water availability and how this might limit biomass production and hence yield. She concluded that high VPD may limit production even in parts of the world where oil palm are not normally considered to suffer from water stress. Furthermore, various studies indicate that VPD above a certain level decreases photosynthesis due to stomatal closure with large VPDs (Brum et al., 2021; Carr, 2011; Dufrene and Saugier, 1993; Meijide et al., 2017). Similar observations were made in an irrigation trial in Ivory Coast where stomata closure was observed during dry, windy periods (Harmattan wind) although soil moisture was maintained high through irrigation (Prioux et al., 1992). Thus, oil palm may be adversely affected not only by dry soils, as estimated here by the WSI, but also by the evaporative demand of the air estimated from the VPD. Our analysis shows that negative yield anomalies were associated with large VPD (Fig. 7) at critical stages of bunch development suggesting that partial stomatal closure when evaporative demand is large may reduce yields at the block level.

The negative relationship between WUE and VPD (Fig. 6) is consistent with widely observed decreases in WUE when evaporative demand is high (Tanner and Sinclair, 1983). The estimation of WUE must be treated with caution as the estimate of ETo does not take into account the reduction of transpiration when stomata partially close in response to higher VPD. Furthermore, the stomatal response to VPD tends to maximize photosynthesis at those times of the day when VPD is small and WUE efficiency is high. Nevertheless, we note that our range of ETo (1127–1194 mm) for SS compares well with the average annual ETo of $1216 \pm 34 \text{ mm y}^{-1}$ measured using eddy-covariance in a 12-year old oil palm plantation in a site located in the same region (Meijide et al.,

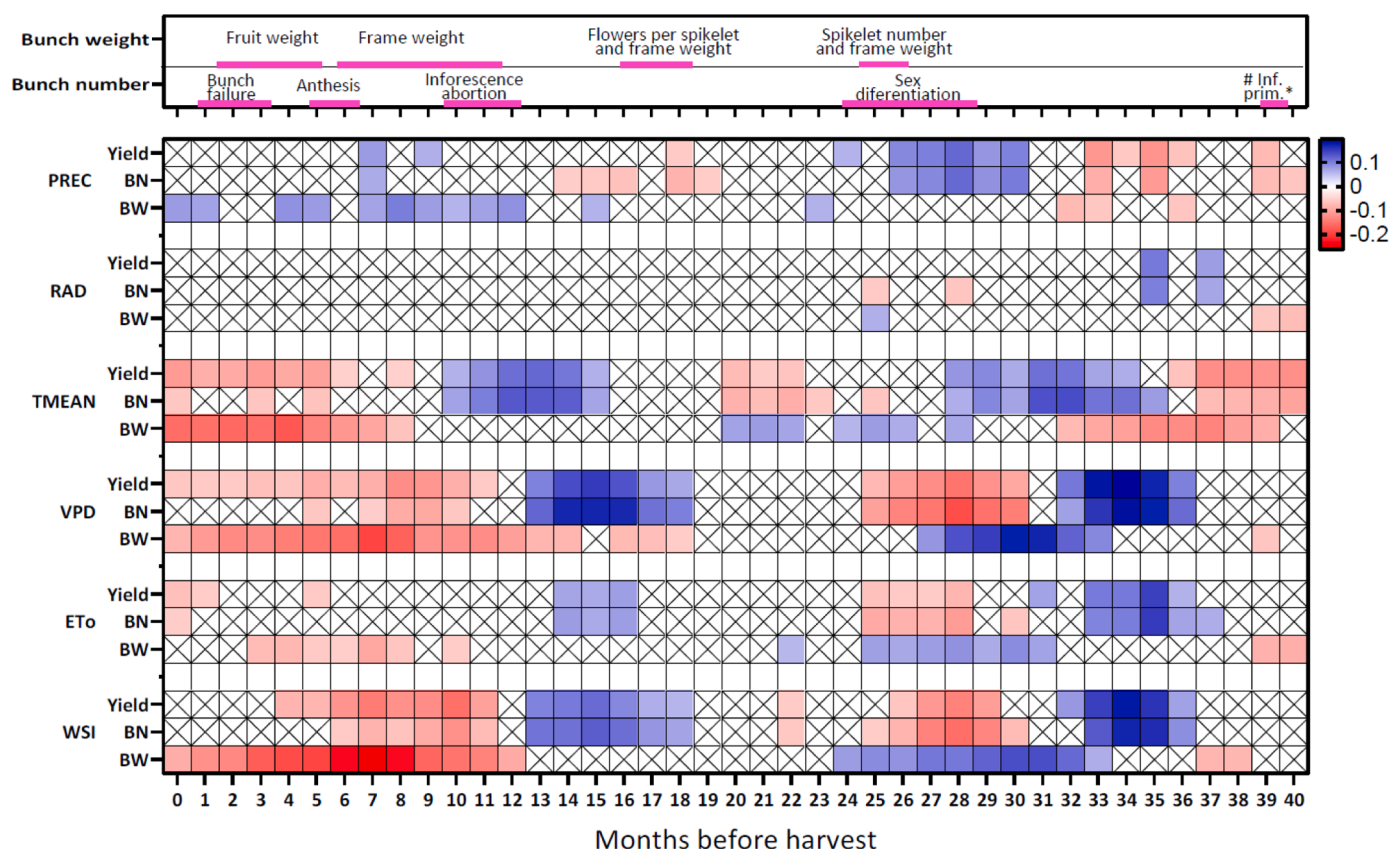


Fig. 7. Heat map showing correlations between monthly anomalies in fresh fruit bunches (FFB) yield, yield components, namely bunch number (BN) and individual bunch weight (BW), and anomalies in monthly meteorological factors including average incident radiation (RAD), mean temperature (TMEAN), daily mean vapor pressure deficit (VPD), total reference evapotranspiration (ET₀), total precipitation (PREC), and average water stress index (WSI). Colors indicate sign and magnitude of the Pearson correlation coefficient, with crosses indicating correlations with $p > 0.05$. Key stages in primordia development are shown at the top (adapted from Breure and Menendez, 1990; Carr, 2011; Adam et al., 2011).

Table 4

Pearson correlation coefficients for the relationships between annual anomalies of fresh fruit bunch (FFB) yield and yield components for current year (k) with the anomalies for the same variables during the subsequent four years. Correlations exhibiting $p > 0.05$ are indicated with crosses.

Variable	Year k + 1	Year k + 2	Year k + 3	Year k + 4
Annual FFB yield	-0.24	-0.36	x	x
Bunch number	-0.37	-0.26	x	x
Bunch weight	0.34	-0.20	-0.26	x

2017). Similarly, our estimated values of WUE for SS (22.0 kg FFB ha⁻¹ mm⁻¹) are consistent with the estimate of WUE derived from our re-analysis of the data of Meijide et al. (2017) for the same region of 22.8 kg FFB ha⁻¹ mm⁻¹.

Smith (1989) suggested that since increasing biomass productivity is an important objective in oil palm breeding, selecting genotypes with low stomatal sensitivity to soil water or to VPD might be advantageous where irrigation is impractical. We suggest that selection for low

stomatal sensitivity may not always be the optimum strategy: stomatal sensitivity to VPD leads to slower depletion of soil water which may be advantageous in some situations. Kholová et al. (2021) suggested that there may be a trade-off between traits that provide a yield advantage in a particular drought context but reduce yield under well-watered conditions. In the case of cassava, a crop with stomata highly sensitive to both VPD and soil water deficit, it has been suggested that varieties with insensitive stomata should be developed for irrigated conditions and for regions where soil water deficits are short and not severe, while varieties with sensitive stomata should be developed for those areas without irrigation and prolonged soil water deficits (Cock and Connor, 2021). Based on the substantial yield reductions associated with large WSI and VPD derived from the analysis of temporal FFB yield variation, oil palm breeders should consider selection of sensitive varieties for areas where soil and air drought are likely to be severe and insensitive varieties for areas with limited and ephemeral soil water deficits.

Large VPD and WSI in the period 25–30 months before harvest (sex determination, spikelet number and frame formation) reduced final BN and increased BW. The greater BW is likely to be the result of

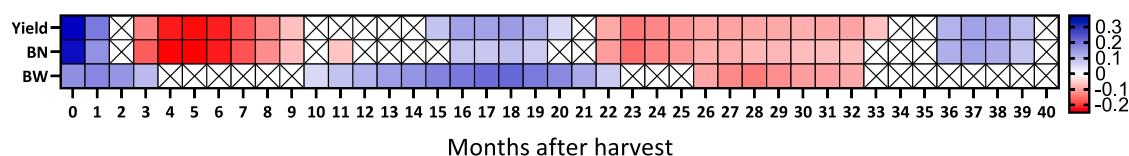


Fig. 8. Heat map showing correlations between actual fruiting activity anomalies and fresh fruit bunch (FFB) yield and yield components anomalies. Correlations exhibiting $p > 0.05$ are indicated with crosses. Colors indicate sign and magnitude of the Pearson correlation coefficient.

compensation in BW when BN is reduced (Corley and Breure, 1992). Stress in the period 12–18 months before harvest, due to unfavorable weather, was associated with increased yield mainly due to increased BN (Fig. 7). Similarly, high fruiting activity had a positive impact on yield in the period 12–18 months after harvest, due to increased BW (Fig. 8). We do not fully understand why these positive associations occur, but we note that other local studies have observed similar trends (Sidhu et al., 2021). In the final six months before harvest, when BN is already largely determined, the main effect of stress is reduced BW and hence FFB yield.

Plantation managers often observe that after highly productive years palms are exhausted and production in the following year is lower. Corley and Breure (1992) referred to this cyclic production which is similar to alternancy in fruit trees. Oil palm trunk may build up substantial reserves of non-structural carbohydrates (NSC) that can be later remobilized in the absence of fresh assimilates (Legros et al., 2006). Furthermore, during periods of strong vegetative growth fresh assimilates are allocated to the NSC reserve pool, whereas during fruit filling reserves are remobilized (Legros et al., 2009). Our studies support the plantation managers' and Corley and Breure's observations that high yields in any one year are associated with lower yields in the following two years (Table 4). We suggest that during years of high production there is a large fruit sink as the bunches rapidly increase in weight and carbohydrate reserves in the stem are remobilized. This would leave the palms, in the words of the plantation managers "exhausted" with insufficient carbohydrates to satisfy the demands of the growing bunches and the newly initiated panicles. A deeper understanding of this cyclic phenomenon would make life easier for the managers of oil palm plantations and those of us who wish to understand how meteorological anomalies influence yield.

5. Conclusions

In this study, WSI was the main driver of variation in FFB yield. We also found a negative association between both yield and WUE with VPD, which is in line with previous reports of decreased stomatal conductance and hence biomass production as VPD increases. We believe that this the first time this phenomenon has been demonstrated for oil palm at the block level. We confirmed the well-known phenomenon of meteorological anomalies up to three years before harvest markedly influencing yield. We also detected strong endogenous yield cycles, in which current FFB yield influences subsequent yields, mainly via effects on BN. The findings of this study can be used to improve current oil palm models and yield forecasting.

Declaration of Competing Interest

The authors declare no conflict of interest. The paper contents have not been previously published nor are under consideration for publication elsewhere. All co-authors have contributed to the paper and have agreed to be listed as co-authors.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108789.

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