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Beyond the Highest-Yielding Variety: Breeding Progress, Yield Architecture, and Climate-Resilient Multi-Trait Selection in Indonesian Oil Palm

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ABSTRACT

Oil palm improvement is frequently discussed as a search for progressively higher fresh fruit bunch (FFB) or crude palm oil (CPO) yield. Such a single-trait perspective is increasingly inadequate because economically successful planting materials must simultaneously express high productivity, early bearing, favourable bunch architecture, manageable vegetative growth, efficient oil recovery, environmental stability, and resistance to major biotic and abiotic stresses. This qualitative literature review integrates contemporary research published primarily during 2020–2026 with an exploratory statistical analysis of 54 Indonesian oil palm varieties released between 1984 and 2017. Catalogue-level analysis reveals a strong negative relationship between bunch number and average bunch weight (Spearman $\rho = -0.885$, $p < 0.001$), a positive association between FFB productivity and reported oil output ($\rho = 0.619$, $p < 0.001$), progressively earlier harvesting in newer releases ($\rho = -0.566$ with release year), and higher reported CPO/oil productivity among later generations. However, environmental contrasts within individual genetic materials demonstrate that maximum recorded yield cannot be interpreted independently of growing environment. Recent genomic selection, GWAS, QTL mapping, transcriptomics, metabolomics, high-throughput phenotyping, and disease-resistance research collectively support a shift toward multi-trait, environment-specific breeding. The review proposes a selection architecture centred on robust lifetime oil productivity rather than maximum short-term yield, integrating productivity, precocity, harvestability, extraction efficiency, genotype × environment stability, climate resilience, disease resistance, and deployment economics.

Keywords

Oil palm, *Elaeis guineensis,* Genetic improvement, Fresh fruit bunch, Crude palm oil, Genomic selection, Genotype environment interaction, Drought tolerance, Ganoderma boninense, Multi-trait breeding.

JEL Classification: Q16; Q12; Q15; Q18; O33

Introduction

Oil palm (*Elaeis guineensis* Jacq.) occupies a distinctive position in global vegetable-oil agriculture because extraordinarily high biological oil productivity can be achieved on a relatively small land area compared with most annual oil crops. This productivity advantage has made oil palm economically important for producing countries while simultaneously creating a strategic challenge: future growth in vegetable-oil supply should increasingly come from higher and more stable productivity on existing agricultural land rather than from proportional expansion of cultivated area. For Indonesia, this challenge is particularly important because increasing productivity can improve farm income and national output while potentially reducing the pressure to expand production spatially. The productivity question is therefore no longer simply how to produce more fruit, but how to obtain greater and more stable recoverable oil from each hectare throughout the economic life of a plantation [1-3].

Genetic improvement is a central component of this intensification strategy. Oil palm breeding has progressed from empirical

selection toward structured recurrent-selection schemes, germplasm enrichment, quantitative genetics, molecular-marker systems, genome-wide association studies (GWAS), quantitative-trait-locus (QTL) mapping, genomic selection, transcriptomics, metabolomics, and increasingly integrated molecular–phenotypic approaches. Yet conventional oil palm breeding remains unusually slow because a complete evaluation cycle requires several years before economically relevant traits can be measured reliably, while new commercial material may require well over a decade to develop and validate. Genomic prediction is particularly attractive in this context because it can potentially identify superior parents or individual palms before complete lifetime phenotypic information becomes available [4-6].

The conventional phrase "high-yielding variety", however, obscures several biological realities. FFB yield is itself a composite phenotype arising largely from bunch number and average bunch weight; oil yield is further conditioned by fruit-to-bunch ratio, mesocarp proportion, oil concentration in mesocarp, extraction efficiency, crop age, environment, and management. A palm producing many relatively small bunches can achieve comparable FFB output to a palm producing fewer, heavier bunches. Likewise, two genotypes producing similar FFB can differ substantially in recoverable oil because of bunch composition and extraction characteristics. GWAS studies demonstrate that oil-to-bunch ratio, average bunch weight, bunch number, fruit composition, and related yield components have partly distinct genetic architectures, reinforcing the need to treat oil yield as an integrated rather than singular phenotype [7-9].

The Indonesian varietal catalogue used as the empirical anchor for this review illustrates these contrasts. The early D × P Sungai Pancur 1 material, released in 1984, was described as producing approximately eight bunches annually at around 25 kg per bunch and oil productivity of approximately 6.7 t ha^{-1} yr^{-1}. Later materials increasingly include more detailed reporting of FFB yield, oil extraction and potential CPO productivity. D × P PPKS 540, for example, was described with mean FFB productivity of 28.1 t ha^{-1} yr^{-1}, laboratory oil-to-bunch content of 32.1%, industrial CPO extraction of 27.4%, and potential CPO productivity of 8.1 t ha^{-1} yr^{-1}. Such differences reflect not only genetic progress but also changes in breeding objectives and trait measurement.

Nevertheless, comparison among catalogue entries must be interpreted cautiously. The listed materials were released in different decades and assessed at different sites, crop ages, soil environments, experimental periods, and sometimes different definitions of "mean" and "potential" yield. Consequently, historical varietal descriptions cannot be treated as if every variety had participated in one randomised common-environment experiment. Their value lies instead in revealing the changing phenotype of commercial breeding targets and generating hypotheses about breeding progress. This distinction between catalogue-level evidence and experimentally controlled varietal comparison is maintained throughout the present review.

Environmental dependence is particularly important. The attached catalogue reports the Topaz 1 material separately on alluvial soil, shallow peat, and deep peat. FFB productivity decreases from approximately 28.7 t ha^{-1} yr^{-1} under alluvial conditions to 26.6 t on shallow peat and 21.4 t on deep peat, while estimated industrial CPO production falls from 7.2 to 6.2 and 4.9 t ha^{-1} yr^{-1}, respectively. The genotype is unchanged, yet realized productivity differs markedly. This simple example captures a central problem in variety ranking: yield is a property of a genotype operating within an environment and management system rather than an intrinsic number permanently attached to a genetic name.

Climate variability makes this distinction increasingly consequential. Drought, irregular rainfall, high temperature, soil limitations, water-table conditions and extreme climate anomalies influence photosynthesis, inflorescence development, bunch formation and subsequent yield. Recent work shows both physiological and genetic variation among oil palm materials in drought responses, while climate-suitability research indicates that future growing conditions cannot be assumed to reproduce historical production environments [10-14].

A second source of divergence between genetic potential and realized output is plantation management. Analysis of 977 independent smallholder fields in Indonesia showed that average farmer yield represented only about 42% of estimated attainable yield, with nutrient management, harvest intervals, pruning, weed control, planting density and planting-material quality contributing to the observed gaps. This implies that genetic improvement cannot substitute for agronomy: a superior genotype planted under poor management may deliver less oil than a moderately improved genotype under effective agronomic management. Conversely, improved genetics magnify the potential return to good management because the attainable-yield ceiling itself becomes higher [1].

The principal argument developed in this article is therefore that oil palm breeding progress should be evaluated through a multi-trait productivity portfolio. The appropriate objective is not maximum observed FFB or CPO in isolation, but high and stable lifetime oil productivity achieved through favourable yield architecture, early economic bearing, efficient oil recovery, manageable plant architecture, adaptation to target production environments, and resilience to disease and climate stress. The review addresses seven related questions: how Indonesian varietal phenotypes have changed through time; how bunch-number and bunch-weight trade-offs construct yield; how FFB and extraction components interact to determine oil output; how genotype × environment (G×E) affects varietal performance; how disease and drought resilience should enter selection objectives; how genomic and other omics technologies can accelerate breeding; and how improved materials should be deployed in differentiated production environments.

Literature Review

From Dura × Pisifera Hybridization to Multi-Trait Breeding

The fundamental commercial architecture of modern African oil

palm is based on the tenera fruit form generated by dura × pisifera crossing. Discovery and exploitation of shell-thickness inheritance transformed commercial production because tenera fruit has a relatively thick oil-bearing mesocarp and reduced shell compared with dura. Subsequent progress has relied heavily on Deli dura maternal materials and a relatively limited set of major paternal genetic backgrounds, including AVROS, La Mé and Yangambi. Modified recurrent-selection and related reciprocal improvement systems exploit combining ability between these complementary groups while attempting to accumulate favourable alleles for FFB yield, bunch composition, oil yield and increasingly secondary traits such as height, oil quality and stress tolerance [3,15-17].

A narrow breeding base, however, eventually constrains genetic gain. Germplasm collections from Africa and *Elaeis oleifera* populations from Central and South America provide opportunities to widen genetic diversity and introduce traits such as compactness, disease tolerance, drought adaptation, oil quality and distinct fruit characteristics. Studies of natural Ghanaian dura, Senegalese germplasm, Tanzanian material, Cameroon collections, Angola germplasm, Zaire populations and *E. oleifera* collections demonstrate substantial variation in yield components, vegetative traits and population structure [18-24].

Molecular assessment confirms that the requirement to broaden commercial genetic pools is not merely theoretical. AFLP-based analysis of Malaysian breeding populations found relatively close relationships in some advanced groups and recommended greater incorporation of diverse genetic resources and intercrossing among genetically differentiated populations. Introgression studies involving Nigerian, Zairean and Cameroonian germplasm crossed with advanced AVROS-derived breeding populations likewise demonstrate that additional diversity can be incorporated without abandoning commercially valuable yield attributes [25,26].

Recent three-way crosses further illustrate this approach. Nor Azwani et al. [27] examined crosses combining MPOB-Nigeria × Deli dura material with AVROS or Yangambi pisifera backgrounds and found significant genetic variation in bunch yield, quality and vegetative traits. Such materials exemplify the transition from preserving a narrow definition of elite germplasm toward deliberately assembling complementary alleles from multiple sources.

Yield as an Architecture of Component Traits

At a given stand density, FFB production is largely determined by bunch number per palm and mean bunch weight, while productive palms per hectare provide an additional multiplicative component at the plantation scale. These traits are not independent: biological resource allocation, canopy architecture, sex ratio, inflorescence development and source–sink relationships can create compensating relationships among yield components. The statistical analysis of the Indonesian catalogue reported later in this article reveals an especially strong inverse association between bunch number and average bunch weight, suggesting that different genetic materials can construct similar production through markedly different architectures.

Independent experimental literature supports the importance of this decomposition. GWAS, linkage mapping and progeny studies have identified loci associated separately with bunch weight, bunch number and oil-related characters, while progeny analyses show substantial genetic variation for these components. A recent genotyping-by-sequencing linkage study likewise mapped yield-related QTLs in oil palm, reinforcing the value of resolving aggregate yield into biologically meaningful component traits [7,8,17,28]. Selection focused solely on a single annual FFB value therefore risks obscuring the biological pathway by which yield is achieved.

This distinction also matters operationally. A genotype producing many smaller bunches may require different harvesting frequency and labour allocation than one producing fewer heavy bunches. Bunch size can affect harvest ergonomics, fruit collection and transport, while bunch frequency influences the penalty associated with delayed harvesting. The desirable balance is consequently context dependent. Breeding for high yield should optimise bunch architecture jointly with plantation labour systems, harvesting technology, planting density and processing logistics.

Oil yield adds another layer. It can be conceptualized approximately as FFB production multiplied by an effective oil recovery fraction, itself influenced by fruit-to-bunch ratio, mesocarp-to-fruit ratio, oil-to-mesocarp concentration and mill extraction. The genetic architecture of oil-to-bunch and related components has been investigated through GWAS in African *E. guineensis*, wild American oil palm and diverse germplasm. These studies identify multiple associated loci rather than one simple "oil yield gene," reinforcing the polygenic and component-based nature of the phenotype [7,9,29].

Vegetative Architecture, Height and Planting Density

High productivity per palm is not necessarily synonymous with high productivity per hectare. Canopy architecture determines light interception, inter-palm competition and feasible planting density. Breure and Siregar [30], working with dura × pisifera testcrosses in North Sumatra, argued that parental selection should consider yield per hectare at the optimal density rather than yield per palm alone, because progenies differ in mature crown size and competition.

Compact germplasm is therefore strategically important. Evaluation of multiple African collections identified sources with short rachis length and reduced annual height increment that could contribute to higher-density planting ideotypes. Newer genomic work has extended this search to SNP markers associated with compactness traits, with a 2025 GWAS identifying 27 markers associated with seven architectural traits across Deli-, Nigeria- and Yangambi-derived families [31,32].

Height also affects economic lifespan. Tall palms become increasingly difficult and costly to harvest even if physiological

yield potential remains acceptable. QTL mapping for height-related traits therefore has an economic meaning extending beyond morphology. Ting et al. [33] identified height-related QTLs in multi-site material, supporting the incorporation of vegetative architecture into molecular breeding. Rao and Chang [34] similarly emphasized specialized fruit and breeding traits such as virescens, illustrating how modern cultivar development increasingly integrates attributes that improve harvesting, processing or management rather than concentrating exclusively on FFB tonnage.

Genomics, Genomic Selection and Omics-Assisted Improvement

Conventional selection in a perennial crop is slow because breeders must wait years for reliable production phenotypes. Genomic selection offers a different decision architecture: genome-wide markers are used to predict breeding values, potentially allowing selection before complete phenotyping. Nyouma et al. [4] demonstrated that genomic predictions could improve selection of hybrid individuals for clonal testing, while Garzón-Martínez et al. [5] found useful prediction accuracies for several morphological and yield-related traits in OxG and backcross populations. Multi-trait models were particularly promising where genetically correlated traits could improve prediction of difficult targets.

GWAS can complement genomic prediction by identifying genomic regions associated with component traits. Babu et al. [7,8] reported marker–trait associations for bunch and oil-yield components, and more recent germplasm work continues to identify markers linked to oil-related phenotypes. Genomic selection and marker-assisted selection should not be viewed as competing systems: the former is attractive for diffuse polygenic variation, while the latter can be especially useful where loci with sufficiently strong and reproducible effects are available.

Genome editing represents a further, potentially complementary layer of improvement. CRISPR/Cas-based approaches could eventually enable targeted modification of genes controlling oil composition, disease response or plant architecture, but oil palm still faces important transformation, regeneration and genotype-specific technical bottlenecks; consequently, genome editing should currently be regarded as a complement to field breeding, marker-assisted selection and genomic prediction rather than a replacement for them [35]. These limitations also reinforce the importance of validating edited or marker-selected material across realistic multi-environment field conditions before commercial deployment.

Transcriptomics moves the analysis closer to biological mechanism. Apriyanto, Compart and Fettke [36] demonstrated developmental changes in mesocarp gene expression associated with starch metabolism and oil accumulation, while a complementary RNA-seq dataset compared leaf gene-expression profiles among palms with different oil yields and genetic backgrounds. These studies imply that yield can eventually be characterized not only by final phenotype but also by molecular signatures operating before the mature production phenotype is completely expressed [36,37].

Metabolomics extends the same logic to metabolic state. Oil palm expresses complex primary and secondary metabolic networks affected by genotype, nutrient status, disease and environmental stress. Nugroho et al. [38] proposed metabolomics-assisted breeding as a route for identifying performance-associated metabolic signatures, while Cui et al. [39] illustrated how metabolomic information could potentially improve precision potassium nutrition. These approaches suggest a future in which breeding and agronomic precision share molecular diagnostic tools rather than operating as isolated disciplines.

Clonal propagation is another route for capturing superior genetic combinations, but it brings both economic opportunity and biological risk. Economic analysis has suggested that high-performing clones can justify a price premium through increased FFB and oil yield, yet tissue culture in oil palm is complicated by the epigenetically associated mantled abnormality. DNA-methylation research identifies changes in the Karma region and other methylation hotspots associated with clonal phenotypes, indicating that propagation quality control must be integrated into clonal deployment [40-42].

Climate Resilience and Genotype × Environment Interaction

Climate resilience transforms G×E from a classical plant-breeding concern into a strategic production requirement. A genotype that achieves exceptional yield under favourable water supply may not retain its advantage under recurrent water deficit. Conversely, materials that sacrifice a small amount of maximum yield but maintain a larger fraction of productivity under stress may generate greater lifetime economic output.

Controlled and field studies confirm substantial variation in drought response. Molecular-marker research has identified candidate genes and SNP variation associated with drought-tolerance mechanisms, including work involving choline monooxygenase. Physiological comparison among *E. guineensis*, *E. oleifera* and OxG materials similarly demonstrates genotype-dependent maintenance of photosynthesis and stomatal behaviour under water deficit [13,43,44].

Multiseasonal yield records are especially valuable because drought effects on oil palm can be delayed. Environmental conditions affecting sex determination and inflorescence development may influence harvests many months later. Hermanto et al. [11] therefore used multiseasonal yield data to evaluate drought tolerance, while Brum et al. [45] examined irrigation effects on oil palm transpiration during ENSO-related drought in the Brazilian Amazon. Climate-anomaly modelling further demonstrates nonlinear productivity responses, which means simple annual rainfall totals may inadequately represent climatic risk [11,14,45].

At larger scales, climate-suitability analyses indicate that crop suitability is likely to shift spatially under climate change. Paterson [46] examined climate suitability for African oil palm production,

while Appelt et al. [12] evaluated climate-change impacts on major tree crops in Southeast Asia. A systematic review by Abubakar et al. [10] and a recent synthesis of climate variability and water stress in Malaysian oil palm both emphasize that irregular rainfall, prolonged dry periods and elevated temperature can constrain biomass production and yield [47]. These findings strengthen the argument that future varieties should be recommended for defined "target populations of environments" rather than marketed as universally optimal materials.

Disease Resistance as Protection of Lifetime Yield

Yield potential that is progressively lost to basal stem rot is not economically equivalent to stable yield. *Ganoderma boninense* resistance must therefore be conceptualized as a productivity trait because it protects stand density, plantation longevity and cumulative oil output.

Research over the last several years increasingly supports quantitative rather than simply binary resistance. Daval et al. [48] identified a complex QTL architecture associated with *G. boninense* resistance, while long-term field evaluation in tropical peat identified genetic materials differing in partial resistance. Molecular screening studies have additionally explored genes and markers associated with basal-stem-rot responses [48-50]. Pathogen-side resources have also improved: a chromosome-scale genome assembly of *G. boninense* provides a stronger basis for identifying pathogenicity-related genes and host–pathogen targets [51]. In parallel, metabolomic profiling has distinguished resistant and susceptible oil palm root responses at nursery stage, supporting the potential use of biochemical signatures alongside genetic markers in resistance screening [52].

The evidence base has advanced further in 2026. Daval et al. [53] integrated QTL mapping with RNA sequencing in Deli and La Mé breeding populations, identifying multiple resistance loci and differentially expressed genes associated with *G. boninense* responses. The study is important methodologically because it connects statistical genetic regions with transcriptional responses in genetically related experimental populations. Faizah et al. [54] likewise reported genetic structuring associated with resistance using markers targeting the EgLCC24 gene. Together these developments strengthen the feasibility of breeding programmes that incorporate resistance markers while continuing selection for yield and agronomic performance.

Fusarium resistance remains relevant beyond Southeast Asia and in international germplasm deployment. Daval et al. [55] identified *Fusarium* wilt resistance loci in two major breeding backgrounds, illustrating that durable global breeding portfolios must accommodate multiple pathogen environments rather than optimising exclusively for the dominant disease of one production region.

Method

Review Design

This study employed a qualitative literature review (QLR) rather than a systematic literature review. The objective was interpretive synthesis: to connect statistical patterns visible in released Indonesian planting materials with contemporary evidence on genetics, genomics, physiology, environmental adaptation and deployment. Consequently, the study did not use PRISMA, formal meta-analysis, or a systematic-review claim of exhaustive literature capture.

Peer-reviewed journal literature published primarily between 2020 and September 2026 was prioritized. Literature was identified purposively through combinations of topic-specific keyword searches, publisher and bibliographic platforms, and citation chaining rather than through a protocol intended to achieve exhaustive retrieval. The thematic search focused on combinations of "oil palm", "*Elaeis guineensis*", "yield", "bunch number", "bunch weight", "oil yield", "genomic selection", "GWAS", "QTL", "germplasm", "compactness", "height", "drought", "genotype environment", "*Ganoderma*", "*Fusarium*", "transcriptomics", "metabolomics", "clonal", and "precision agriculture". Preference was given to empirical studies from established peer-reviewed journals and to studies directly linked with breeding, yield formation, resilience or deployment. This purposive strategy is consistent with the interpretive aim of a qualitative literature review and should not be interpreted as evidence of systematic-review completeness.

The reviewed evidence was organized into eight interpretive domains: historical breeding progress; yield architecture; oil-production efficiency; vegetative architecture; G×E and climate resilience; biotic resilience; genomic and omics-enabled breeding; and deployment economics. Literature was included when it contributed directly to one or more of these domains. Studies representing contrasting genetic backgrounds and geographical production systems were retained because the purpose was to understand the general breeding problem rather than restrict the review to a single country.

Statistical Treatment of the Indonesian Varietal Catalogue

The empirical component was based on 54 oil palm varieties or released materials contained in the attached Indonesian varietal-description catalogue, covering release years from 1984 to 2017. The catalogue provides different combinations of release year, age at first harvest, annual bunch number, average bunch weight, FFB productivity, oil/CPO productivity, industrial extraction rate, mesocarp percentage, oil-to-mesocarp percentage, vertical growth rate and selected oil-quality characteristics.

Where a characteristic was reported as a range, the midpoint was used for descriptive cross-variety calculations. This transformation was used only to summarize catalogue structure and does not imply that the midpoint equals the underlying experimental mean. "Reported oil/CPO productivity" combined directly reported oil yield and potential CPO values for an initial exploratory analysis. Because this mixture can inflate apparent historical change, sensitivity analyses separated entries explicitly reported as mean/current values from those reported as potential values.

Varieties were divided into three descriptive release periods: 1984–1999, 2000–2009 and 2010–2017. Medians were calculated because several traits had asymmetric distributions and because catalogue entries were not generated under a common experimental design. Spearman rank correlations were used to examine monotonic relationships among release year, harvest age, bunch number, bunch weight, FFB productivity and CPO/oil output. Kruskal–Wallis analysis provided an exploratory comparison of CPO/oil distributions across release periods.

These tests should not be interpreted causally. Release year is correlated with breeding generation, changes in evaluation methods, changes in trial environments and changes in trait-reporting conventions. Accordingly, statistical significance is used to identify patterns deserving biological interpretation rather than to establish a controlled estimate of annual genetic gain.

Results

Descriptive Structure of the Released-Variety Dataset

Across the 54 entries, median age at first harvest was approximately 26 months, median bunch number was 18.3 bunches palm^{-1} yr^{-1}, median average bunch weight was approximately 12.3 kg, and median reported CPO/oil productivity was approximately 7.5 t ha^{-1} yr^{-1}. For varieties with comparable FFB information, median mean FFB productivity was approximately 27.9 t ha^{-1} yr^{-1}. Considerable variation was also present in vertical growth rate, mesocarp fraction and oil-to-mesocarp concentration.

The broad trait variation confirms that commercial oil palm improvement has generated multiple phenotype combinations rather than convergence toward one uniform plant type. Some genetic materials emphasize large bunches; others express high bunch frequency. Some show relatively high oil concentration, while others achieve high hectare-level oil productivity through FFB production. Recent genetic-diversity studies similarly show that exploitable variation remains available within advanced and germplasm populations [18,19,23,24].

Earlier Economic Bearing in More Recent Releases

Release year was negatively associated with age at first harvest (Spearman $\rho = -0.566$, $p < 0.001$). Median harvest age declined from approximately 30 months in the 1984–1999 group to 26 months in 2000–2009 and 24 months in 2010–2017.

Figure 1 summarizes this shift in median first-harvest age across release periods. It should not be interpreted as a controlled estimate of genetic gain per year, because older and newer materials were not evaluated under identical conditions. Instead, it illustrates how commercial breeding targets increasingly incorporated precocity alongside mature production.

The economic significance of this shift extends beyond biological curiosity. Earlier harvesting shortens the non-revenue phase following field establishment and can improve discounted plantation returns, particularly in replanting programmes where growers temporarily lose income from mature palms. Precocity is nevertheless valuable only when it does not compromise later productivity, canopy structure, or plantation lifespan. Selection should therefore focus on early economic production rather than simply the earliest fruit initiation.

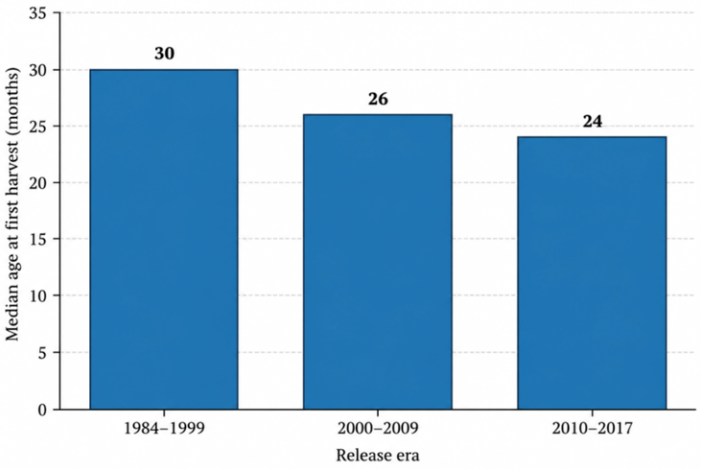


Figure 1: Earlier Economic Bearing Across Oil Palm Release Eras.

A Strong Bunch-Number versus Bunch-Weight Trade-Off

The strongest statistical relationship in the catalogue was the inverse association between annual bunch number and mean bunch weight ($\rho = -0.885$, $p < 0.001$; $n = 51$). This relationship is sufficiently strong to challenge the idea that "high yield" represents a single morphological solution.

Figure 2 plots annual bunch number against average bunch weight. The distribution forms a clear descending pattern: materials positioned at the high-bunch-number end tend to produce lighter bunches, while those with very heavy bunches generally produce fewer annually.

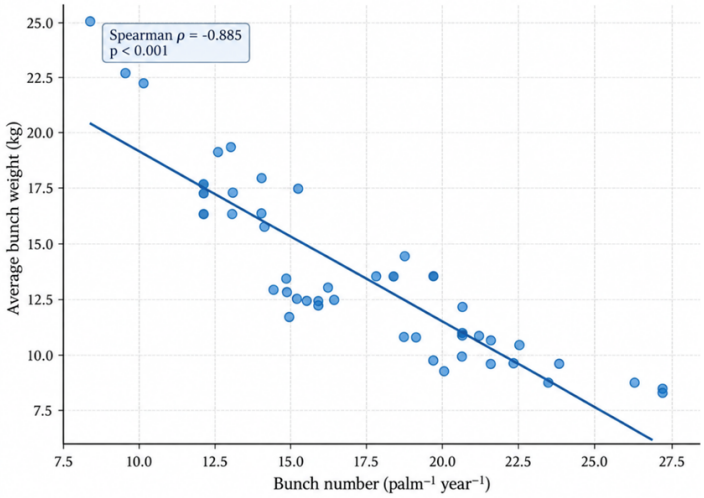


Figure 2: Yield Architecture Trade-Off—More Bunches, Lighter Bunches.

The figure demonstrates that breeding should evaluate yield architecture, not merely final tonnage. A material with 20 relatively light bunches and another with 12 heavy bunches can occupy

similar FFB productivity classes but impose different harvesting requirements. This result is consistent with genetic evidence identifying distinct loci and heritable variation for bunch number and bunch weight [7,8,17]. The practical optimum will vary with labour availability, harvesting technology, crop age and plantation design.

This observation also provides a useful explanation for apparent generational change. Median bunch number increased from approximately 12.0 in the earliest release group to 16.4 in the 2000–2009 group and 20.0 in 2010–2017, whereas median bunch weight did not increase proportionally. Newer materials therefore appear, in part, to build productivity through a changed balance among yield components rather than by simply enlarging bunches.

FFB Productivity and Recoverable Oil

Mean FFB productivity was positively associated with reported CPO/oil productivity ($\rho = 0.619$, $p < 0.001$, $n = 41$). The relationship remained positive when the analysis was restricted to entries reported as mean/current rather than potential CPO values. This supports a straightforward but important conclusion: despite increasing interest in oil concentration and extraction characteristics, hectare-level FFB productivity remains a major proximate driver of hectare-level oil production.

Figure 3 visualizes the positive FFB–oil relationship. The scatter also shows substantial vertical dispersion, indicating that comparable FFB productivity does not inevitably translate into identical CPO output.

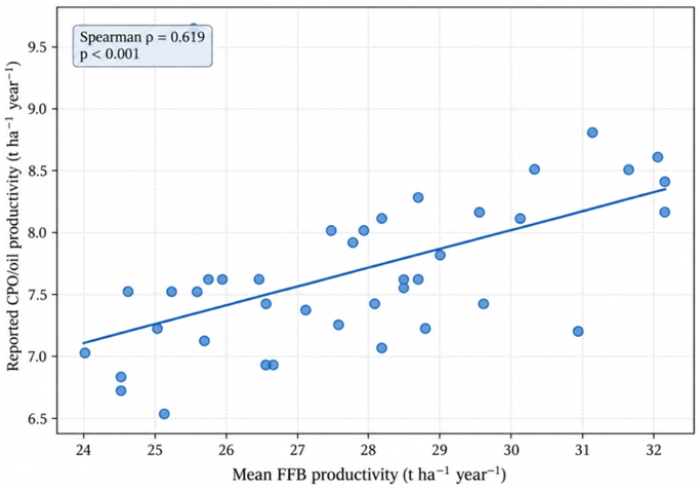


Figure 3: Fresh Fruit Bunch Productivity as a Proximate Driver of Oil Output.

The dispersion around the relationship is biologically important. It represents, among other factors, differences in bunch composition, oil content, industrial extraction, maturity, and reporting method. Breeding for CPO yield must therefore combine FFB productivity with effective oil recovery. This interpretation agrees with GWAS results in which oil-to-bunch and bunch-yield components are influenced by overlapping but non-identical genomic regions [7,9,29].

By contrast, oil-per-mesocarp percentage alone showed essentially no monotonic relationship with catalogue-level CPO/oil productivity ($\rho = -0.077$, $p = 0.584$). A high oil concentration in mesocarp is therefore insufficient if the palm produces fewer bunches, inadequate FFB biomass, unfavourable fruit-to-bunch characteristics, or lower effective extraction. The breeding target should be a system phenotype—oil recovered per hectare over time—rather than the maximum value of any one component.

Evidence of Historical Productivity Improvement

Release year showed a positive association with combined reported CPO/oil productivity (Spearman $\rho = 0.620$, $p < 0.001$, $n = 54$). Median catalogue values increased from around 6.7 t ha^{-1} yr^{-1} in the 1984–1999 group to 7.5 t ha^{-1} yr^{-1} in 2000–2009 and 8.15 t ha^{-1} yr^{-1} in 2010–2017. The exploratory Kruskal–Wallis comparison across release periods was also significant, $H(2) = 21.82$, $p < 0.001$, indicating a distributional shift among release cohorts while not establishing a causal annual rate of genetic gain.

However, because later catalogues more frequently report "potential" CPO values, a sensitivity analysis is necessary. Among 31 entries categorized as mean/reported rather than potential yield, release year remained positively correlated with oil output ($\rho = 0.468$, $p = 0.0079$), with median values of approximately 6.7, 7.4 and 7.5 t ha^{-1} yr^{-1} across the three release periods. Among 23 potential-yield entries, release year was likewise positively related to potential CPO production ($\rho = 0.496$, $p = 0.016$), with the median increasing from around 7.53 t ha^{-1} yr^{-1} for 2000–2009 releases to 8.45 t ha^{-1} yr^{-1} for 2010–2017 releases. This separation reduces, although it cannot eliminate, the risk that changing reporting conventions alone explain the temporal pattern.

These findings strengthen the interpretation of historical breeding progress but should not be converted into a formal annual genetic-gain estimate. Experimental studies provide more appropriate estimates of genetic gain because they control pedigree and trial structure. Tupaz-Vera et al. [56], for example, specifically evaluated genetic progress among oil palm progenies, while modern breeding studies continue to quantify heritability, parental performance and combining ability in defined populations.

Age at first harvest was also negatively related to oil productivity ($\rho = -0.578$, $p < 0.001$), with an even stronger negative relationship in the mean/reported-yield subset. The interpretation should again be cautious: early harvest does not necessarily cause higher mature yield. Instead, modern breeding appears increasingly to package early bearing and high productivity in the same commercial materials.

Genotype × Environment Effects: The Topaz Example

The strongest warning against universal varietal ranking comes from environmental differentiation. Topaz 1, evaluated across contrasting soil environments in the original catalogue, produced approximately 28.7 t FFB ha^{-1} yr^{-1} on alluvial soil, 26.6 t on

shallow peat, and 21.4 t on deep peat. Corresponding industrial CPO production was approximately 7.2, 6.2 and 4.9 t ha^{-1} yr^{-1}.

The difference between 7.2 and 4.9 t CPO ha^{-1} yr^{-1} is approximately one-third of the higher value. This environmental effect is large enough to overshadow many of the differences used to distinguish commercially promoted varieties. G×E research in oil palm therefore has direct deployment implications. Castañeda-Garzón et al. [57] documented G×E effects in *E. guineensis* and OxG materials, while climate, drought and multiseasonal analyses demonstrate that genotypic performance stability should be explicitly evaluated rather than inferred from single-environment performance [11,13].

Figure 4 presents these data as an environmental performance gradient. The purpose is not to generalize one historical Topaz trial to all peat or alluvial environments, but to demonstrate the magnitude by which environmental context can alter the observed productivity of one genetic material.

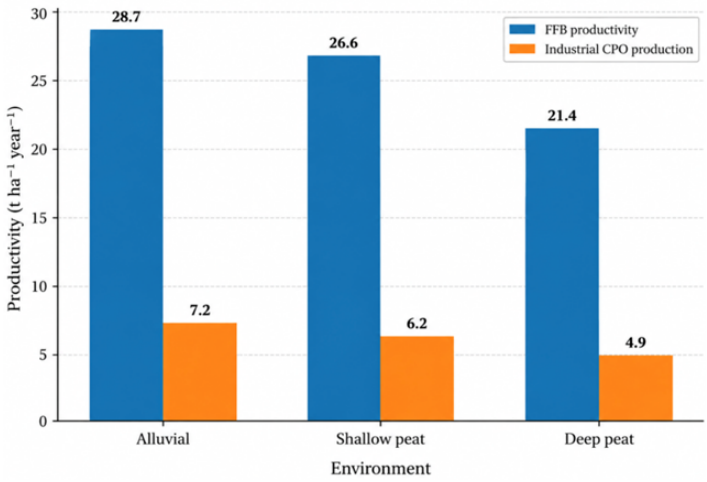


Figure 4: Environment-Dependent Performance of Topaz 1.

Architecture and Harvestability as Productivity Traits

Vertical-growth rate in the catalogue varies substantially among varieties. This variation has implications for harvesting cost, accessibility and plantation lifespan. Palms with high early yield but rapid height increment may become economically difficult to harvest sooner than slower-growing materials. Conversely, excessively compact materials should not be selected at the expense of adequate canopy photosynthesis or yield.

Modern breeding increasingly treats compactness as a quantitative selection objective. Germplasm evaluations have identified short-rachis and low-height-increment sources, while GWAS has identified SNP associations for rachis length, petiole morphology and related architecture traits. Breure and Siregar [30] further showed why the economically relevant measure is hectare-level yield at appropriate density rather than per-palm yield in isolation.

From Phenotype to Digital and Molecular Phenotyping

Modern breeding increasingly generates data streams beyond manual field measurement. Satellite imagery, UAV imagery and machine learning can estimate stand characteristics, detect palms, and contribute to yield prediction. Watson-Hernández et al. [58] demonstrated oil palm yield estimation using vegetation and humidity indices combined with machine-learning techniques, while Putra and Wijayanto [59] reported high accuracy for object-based deep-learning detection and counting of palms from high-resolution imagery. Hilal et al. [60] likewise developed neural-network approaches for predicting FFB yield using environmental and plantation variables.

These technologies do not replace genetic evaluation, but they can reduce phenotyping cost, improve temporal resolution, and allow breeders to quantify traits across larger populations and more environments. Their greatest contribution may ultimately emerge when high-throughput field phenotypes are integrated with dense genomic information.

Discussion and Analysis

Breeding Progress Is Real but Cannot Be Reduced to a Yield Ranking

The Indonesian catalogue provides evidence consistent with long-term breeding progress: newer releases tend to bear economically earlier, produce more bunches, and report higher oil output. This interpretation is supported by breeding literature documenting continued genetic gain, development of new cultivars, exploitation of recurrent selection and introduction of new germplasm [3,27,56].

However, an ordinal list from “highest yielding” to “lowest yielding” would be methodologically misleading. Historical entries do not share a common environmental denominator. Some values are averages, some potentials; some were derived from early mature periods and others from later production stages; some explicitly represent poor or specialized sites. A 9 t ha^{-1} yr^{-1} CPO value recorded as potential production at a favourable stage cannot legitimately be declared superior to a 7.5 t value measured as a multiyear mean in another environment without further normalization.

The scientifically useful signal is therefore directional rather than ordinal. Selection has progressively combined higher oil output with earlier production and a wider portfolio of secondary traits. The relevant breeding question is not which catalogue entry has the largest number, but which biological attributes explain progress and can be reproduced robustly in future target environments.

The Bunch Trade-Off Changes How Yield Should Be Interpreted

The $\rho = -0.885$ relationship between bunch number and bunch weight is more than a statistical curiosity. It indicates a fundamental resource-allocation structure. Increasing one yield component may be accompanied by compensation in another. Breeders therefore need a selection index that rewards total and stable oil production without unintentionally moving component

traits toward operationally undesirable extremes.

For example, numerous small bunches may support high FFB output but require high harvesting frequency and efficient logistics. Very heavy bunches can raise harvest difficulty and may create another set of labour and handling constraints. The optimal architecture depends partly on whether harvesting remains predominantly manual or becomes increasingly mechanized.

This finding also helps explain why single-component marker discovery is not equivalent to improvement. A marker increasing bunch number is valuable only in the context of its effects on bunch weight, oil content, plant architecture and lifetime productivity. Genomic selection is particularly attractive under such circumstances because it can incorporate information distributed across many loci and potentially predict aggregate breeding value rather than optimise one marker at a time [4,5].

The Appropriate Objective Is Recoverable Oil per Hectare over the Plantation Life Cycle

A more defensible hierarchy of breeding objectives begins with cumulative recoverable oil per hectare, not FFB alone. FFB is a major driver of CPO, as demonstrated by the observed $\rho = 0.619$ relationship, but an oil palm plantation is economically valuable because of harvested and processed oil. A simple life-cycle representation can therefore connect yield architecture, productive stand density and effective oil recovery in one expression [7,9].

$$LOY = (1/1000) \sum_{t=1}^{T} (B_t \times W_t \times D_t \times ER_t)$$

In this expression, LOY is cumulative lifetime recoverable oil in tonnes per hectare; B_t is bunch number per palm in year t; W_t is mean bunch weight in kilograms; D_t is the number of productive palms per hectare, thereby incorporating stand survival or attrition; ER_t is the effective oil-recovery fraction; and T is the length of the productive evaluation period. The factor 1/1000 converts kilograms to tonnes when W_t is expressed in kilograms. This formulation changes several breeding priorities because precocity brings revenue forward, slower height increment can extend harvestable life, disease resistance preserves productive stand density, drought stability reduces severe yield losses, and higher recovery efficiency converts a larger share of harvested biomass into commercial oil. None of these traits is fully captured by maximum FFB in a short evaluation window.

Oil palm breeding should consequently distinguish peak yield, mean mature yield, yield stability, and cumulative lifetime yield. A genotype with a slightly lower peak but substantially greater disease survival or drought stability could outperform a nominally higher-yielding genotype over 20–25 years. This is especially relevant for *Ganoderma* resistance, where yield protection may be more economically important than modest differences among healthy palms.

Precocity Should Be Valued Economically, Not Biologically Alone

The reduction in median age at first harvest from approximately 30 months to around 24 months across catalogue eras potentially changes plantation cash-flow profiles. For large estates, a six-month reduction in the non-revenue period affects capital recovery across thousands of hectares. For smallholders, the social significance can be greater because replanting temporarily removes an established source of household income.

Yet breeding for extreme precocity could be counterproductive if it reallocates resources away from root development, trunk stability, canopy development or later productivity. The proper metric is therefore not “months to first fruit” but net economic benefit generated by the entire yield curve. Breeding trials should increasingly report age-specific cumulative FFB and CPO, permitting calculation of discounted economic productivity rather than reporting first harvest and peak yield as disconnected variables.

Genotype × Environment Must Move from Statistical Afterthought to Deployment Principle

The Topaz example demonstrates that environment can change CPO productivity sufficiently to alter apparent varietal ranking. G×E analysis therefore should not be relegated to a supplementary ANOVA table. It should define where planting materials are recommended.

A future Indonesian variety-release framework could classify major target production environments using rainfall distribution, drought probability, soil mineralogy, peat characteristics, drainage regime, altitude, disease pressure and possibly heat stress. Multi-environment genetic trials could then estimate not only mean yield but reaction norms and stability parameters. Materials could be identified as broad-adaptation cultivars or as specialist cultivars optimised for particular environmental clusters.

Cock et al. [2] similarly argued for distribution of genetically improved planting material suited to local conditions. This logic becomes more important under climate change because historical plantation zones will not remain environmentally stationary. Climate projections and observed nonlinear climate–yield responses suggest that tomorrow's target environment may differ materially from the environment in which a breeding population was originally selected [2,12,14].

Climate-Resilient Breeding Requires Both Avoidance and Tolerance Traits

Drought resilience is not a single mechanism. Palms can differ in rooting, stomatal regulation, osmotic adjustment, leaf area development, carbohydrate allocation, reproductive sensitivity and recovery after water stress. The ideal breeding strategy should therefore combine physiological phenotyping, long-term yield records and molecular information.

Molecular-marker studies targeting drought-related pathways

provide useful candidate tools, but controlled seedling tolerance must ultimately predict adult field performance before it can become a high-value commercial selection criterion. The same principle applies to photosynthetic performance. Maintenance of photosynthesis under controlled drought is mechanistically informative, but breeding value depends on whether the trait translates into stable bunch formation and oil yield under multi-season field drought.

This argues for a nested testing strategy: rapid nursery screening can eliminate highly susceptible materials; intermediate molecular and physiological screening can enrich promising populations; and long-term multi-environment trials should validate economic yield stability. Nuanlaong et al. [43], Suraninpong et al. [44], Hermanto et al. [11], Montoya et al. [13] and Idris et al. [47] collectively provide components of such an integrated framework. Recent long-term Indonesian fertilization trials further show that better plant nutrition can raise average yield but has limited capacity to prevent yield losses during water-stress periods, underscoring the need to combine genetic resilience with agronomic management rather than assuming that one can substitute for the other [61].

Disease Resistance Should Be Converted into a Yield-Protection Index

Ganoderma breeding illustrates why conventional trait categories can be misleading. Resistance is frequently reported as disease incidence, symptom score, mortality or pathogen response. A grower, however, experiences disease economically through lost palm-years, reduced stand density, premature replanting and reduced cumulative CPO.

Future breeding trials could therefore translate resistance measurements into a yield-protection index combining survival probability, disease progression, age at infection and estimated foregone CPO. Such an index would allow direct comparison between resistance gains and conventional yield gains.

Recent QTL and transcriptomic integration makes this goal increasingly realistic. Daval et al. [53] identified separate resistance loci in Deli and La Mé backgrounds and candidate transcriptional responses linked to those loci. The lack of complete overlap between populations reinforces the view that resistance is complex and population dependent rather than a universal major-gene trait.

The 2026 EgLCC24 study also supports a multi-marker perspective, identifying structured genetic differentiation between resistant and susceptible materials. Combined with earlier field and QTL evidence, this suggests that resistance breeding should integrate multiple evidence layers—phenotypic screening, field survival, linked markers and gene-expression responses—rather than relying on one diagnostic locus [24,48,49].

Genomics Is Most Valuable When It Shortens the Selection Cycle

For annual crops, genomic selection can save one or several seasons. In oil palm, it can potentially save years. This difference makes prediction accuracy economically valuable even when it is imperfect. A genomic model that eliminates inferior candidates before expensive long-term field testing can increase selection intensity while reducing land and time requirements.

However, prediction models are population-dependent. Garzón-Martínez et al. [5] showed that accuracy declined when training and prediction populations were genetically mismatched. This finding should temper expectations of a universal genomic model. Indonesia's breeding programmes may therefore benefit from large interconnected training populations, harmonized phenotyping protocols and longitudinal databases linking pedigrees, SNPs, environment and production.

GWAS markers can complement this system where reproducible associations exist for high-value traits such as compactness, disease resistance or quality. The 2025 compactness GWAS is particularly relevant because architecture is expensive and slow to phenotype: palms must reach sufficient age before crown and height differences become agronomically meaningful. Early DNA-based enrichment for favourable alleles could therefore shorten one of the slowest components of architectural breeding.

Omics Can Bridge the Gap between Genotype and Complex Phenotype

Genomics predicts inherited potential; transcriptomics and metabolomics provide information about how that potential is expressed. In oil-rich fruit tissue, transcriptomic analysis can identify developmental processes associated with carbohydrate allocation and lipid accumulation. In leaves, gene-expression profiles may reveal physiological differences associated with productivity. Metabolomics can characterize downstream biochemical states resulting from both genotype and environment.

The practical challenge is dimensionality. Thousands of molecular features may be measured while breeding populations remain relatively modest. Machine learning can help reduce these data to predictive signatures, but validation across seasons, sites and genetic backgrounds is essential. The most useful omics marker will not be one that discriminates two experimental groups perfectly in one trial, but one that adds predictive value to existing genomic and phenotypic models across relevant breeding populations.

Nugroho et al. [38] therefore appropriately frame metabolomics as a complementary breeding resource rather than an independent replacement for field selection. Cui et al. [39] extend this integration into nutrient management, suggesting that the boundary between breeding and precision agronomy may become increasingly porous.

Planting Material Alone Cannot Close the Productivity Gap

The genetic ceiling and realized farm yield must remain analytically separate. Monzon et al. [1] found independent-smallholder yields averaging only 42% of attainable levels across six Indonesian production regions, with nutrient management, harvesting frequency, weed control, pruning, density and planting material all

contributing to yield gaps. More recent paired-field experiments across five Indonesian provinces found that better management practices increased annual FFB yield by approximately 40% and profit by about 20%, demonstrating that substantial gains can be realized without changing planting material when management constraints are addressed [62]. Together, these studies show why realized farm performance should not be used as a direct proxy for genetic merit.

This has two implications. First, breeding success should not be judged by farm-average yield shortly after the release of a variety unless management quality is controlled. Second, replanting programmes that distribute improved material without agronomic support may capture only a fraction of expected genetic gain.

The correct policy unit is therefore a technology package, comprising authenticated superior planting material, site matching, soil and nutrient diagnosis, correct planting density, effective harvesting, pest and disease management, and data-supported extension. Genetic improvement raises attainable productivity; agronomic systems determine what fraction of that potential becomes commercial CPO.

Precision technologies can support this integration. Remote-sensing detection, machine-learning yield estimation and environmental monitoring could enable early identification of plantations performing below genotype-specific expectations. Watson-Hernández et al. [58], Putra and Wijayanto [59], and Hilal et al. [60] demonstrate the rapid expansion of these digital approaches.

Proposed Multi-Trait Selection Architecture

The statistical and literature synthesis supports a selection framework organized around seven interacting domains rather than a single yield ranking. The first four domains are productivity, represented by FFB, CPO and cumulative lifetime oil output; precocity, represented by age-specific production and speed of economic return; oil-recovery efficiency, represented by fruit composition, mesocarp oil and industrial OER; and architecture and harvestability, represented by height increment, rachis and crown dimensions, and feasible planting density. These domains capture how much harvestable biomass and oil a genotype can produce and how efficiently that production can be maintained operationally.

The remaining three domains are abiotic resilience, including drought, soil constraints, climate anomalies and recovery; biotic resilience, particularly resistance or tolerance to *Ganoderma* and *Fusarium*; and stability and economics, including G × E performance, survival, management compatibility and discounted economic output. Together, the seven domains define a multi-dimensional selection problem in which the economic value of one trait depends on the state of the others, making environment-specific weighting more defensible than a universal single-trait threshold.

Figure 5 integrates these seven domains around the central objective of sustainable lifetime oil production. The arrows point toward the aggregate outcome rather than forming a simple linear breeding pipeline because each domain modifies the value of the others; for example, high peak yield has less lifetime value when disease, excessive height growth or climatic instability shortens productive performance. The framework therefore functions as a conceptual selection architecture rather than as a fixed numerical index.

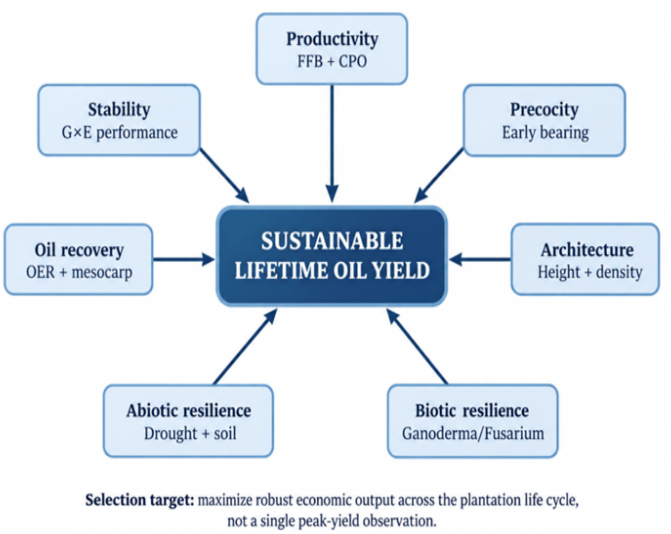


Figure 5: Proposed Multi-Trait Oil Palm Selection Architecture.

The framework implies that a breeding candidate need not achieve the maximum observed value for every component. Multi-trait improvement inevitably involves trade-offs. The objective is a genotype located near a desirable multi-dimensional frontier: high enough FFB, high oil recovery, acceptable bunch architecture, controlled height, good stress stability and adequate resistance. The appropriate weights will depend on the target production environment and production system.

For example, in a high-*Ganoderma*-pressure region, disease resistance should receive greater economic weight than a small difference in peak FFB. In drought-prone environments, yield stability and recovery may outweigh maximum yield under wet conditions. In labour-constrained estates, compactness and harvestability may justify a different balance between bunch number and bunch weight. The framework therefore replaces the idea of a universal "best" variety with the concept of the best-matched breeding portfolio for a defined production environment.

Implications for Indonesian Replanting

Indonesia's replanting challenge provides an immediate application. Replanting replaces decades-old genetics only once every plantation cycle; a poor planting-material decision can therefore impose opportunity costs for twenty years or more. Selection based simply on promotional maximum-yield figures is insufficient.

A stronger replanting system would combine certified genetic identity with environment-specific recommendation zones. Nurseries and growers could receive not merely the variety name but a standardized profile describing expected harvest age, mature FFB range, potential OER, growth increment, target density, drought response and documented disease-resistance evidence.

Such information would improve transparency while creating incentives for breeding organizations to generate comparable multi-environment data. It would also reduce the temptation to treat one record-breaking yield observation as the primary measure of varietal quality.

Economic analysis of clonal material illustrates the same principle. Clones can justify greater initial cost when yield advantages are sufficiently large, but their commercial value depends on reliable propagation quality and avoidance of epigenetic abnormalities [40,41]. A deployment decision therefore requires joint consideration of genetic gain, quality assurance and economic return.

Conclusion and Recommendations

The Indonesian varietal record and contemporary breeding literature tell a consistent story: oil palm improvement has moved beyond the original transformation associated with the dura × pisifera system toward increasingly sophisticated combinations of yield, precocity, architecture, oil recovery and resilience. Exploratory analysis of 54 released materials indicates progressively earlier harvesting and higher reported oil output in later release generations, together with a very strong negative bunch-number/bunch-weight relationship. These patterns suggest that genetic progress has been achieved partly through reconfiguration of yield architecture rather than a simple linear increase in every component simultaneously.

The strongest practical conclusion is that the highest recorded yield should not be equated with the best planting material. Yield is environmentally contingent, age dependent and component based. The same genotype can show substantially different productivity across soil environments, while disease and drought can alter lifetime economic output in ways that a short-term yield maximum fails to capture.

Future selection should therefore target robust lifetime recoverable oil per hectare. This requires integration of FFB productivity, oil extraction, early bearing, growth architecture, harvestability, disease resistance, climate resilience and G×E stability. Economic weighting can convert these biological traits into environment-specific selection indices.

Genomic selection, GWAS and marker-assisted selection offer important opportunities to shorten breeding cycles and increase selection intensity, but their value depends on high-quality multi-environment phenotypes and genetically relevant training populations. Transcriptomics and metabolomics can deepen understanding of oil accumulation, nutrition and stress responses, while remote sensing and machine learning can increase the scale and temporal resolution of phenotyping.

Disease-resistance breeding should be interpreted as yield protection. The recent integration of long-term QTL data with RNA sequencing for *Ganoderma* resistance represents an especially important methodological development because it connects genetic regions, biological responses and breeding populations. Similar integration is needed for drought and other climate-sensitive traits.

For Indonesia, improved genetics should be deployed as part of a broader intensification package rather than as a stand-alone intervention. Certified planting material, site-specific genotype recommendation, correct density, nutrient management, timely harvesting, disease management and precision monitoring must operate together. This integration is particularly important for smallholders, where realized yields remain far below attainable levels in many fields.

Ultimately, the next generation of oil palm improvement should not seek one universally "highest-yielding variety". It should develop diversified, multi-trait breeding portfolios matched to distinct production environments and capable of sustaining high oil output throughout the plantation life cycle. Such a transition offers a more scientifically defensible and economically resilient route for increasing palm oil productivity without relying proportionally on additional land.

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