

Review

Potential of Omics to Control Diseases and Pests in the Coconut Tree

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Abstract: The coconut palm (*Cocos nucifera* L.) is a common crop in pantropical areas facing various challenges, one of them being the control of diseases and pests. Diseases such as bud rot caused by *Phytophthora palmivora*, lethal yellowing caused by phytoplasmas of the types 16SrIV-A, 16SrIV-D or 16SrIV-E, among others, and pests like the coconut palm weevil, *Rhynchophorus vulneratus* (Coleoptera: Curculionidae), and the horned beetle, *Oryctes rhinoceros* (Coleoptera: Scarabaeidae), are controlled by applying pesticides, pheromones and cultural control. These practices do not guarantee eradication since some causal agents have become resistant or are imbedded in infected tissues making them difficult to eradicate. This review condenses the current genomics, transcriptomics, proteomics and metabolomics studies which are being conducted with the aim of understanding the pathosystems associated with the coconut palm, highlighting the findings generated by omics studies that may become future targets for the control of diseases and pests in the coconut crop.

Keywords: *Cocos nucifera* L.; “omics”; pests; insects; diseases; pathogens



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1. Introduction

Of the many common names that the coconut tree (*Cocos nucifera* L.; Areaceae) receives, perhaps the most appropriate are “the tree of life” and “the plant of a thousand uses”, since every part of the plant is useful. The fibers, leaves and wood can be used to produce furniture for the home, brooms, brushes, and even sheds and rustic fences [1]. Handicrafts [2] are made with its dried fruit (Figure 1), and activated carbon is produced from the shell (endocarp) or “coconut bone”. The dried coir (mesocarp) is used as an ecological fiber for padding seats or as an inert soil substrate in agriculture [3].

The fruits of the coconut palm are the most commonly used parts; water (liquid endosperm) is obtained from them, which is consumed fresh or packaged for sale and export due to its nutritional value and mineral balance [4,5]. Additionally, products such as coconut oil, flour, sugar and coconut milk are obtained from “coconut meat” (solid endosperm) [6]. Together, local use, as well as the exportation of these products, are the reason for the high appreciation of the coconut tree around the world [7].

The coconut palm grows in tropical and pantropical areas of the world. The area cultivated with coconut palms comprises ~12 million hectares and supports approximately 80 million people in about 90 countries [8,9]. In the international market, the main producers of coconut are Indonesia, India and the Philippines (Figure 2). In Latin America, Brazil and Mexico occupy the fourth and eighth positions in the world, respectively [8].

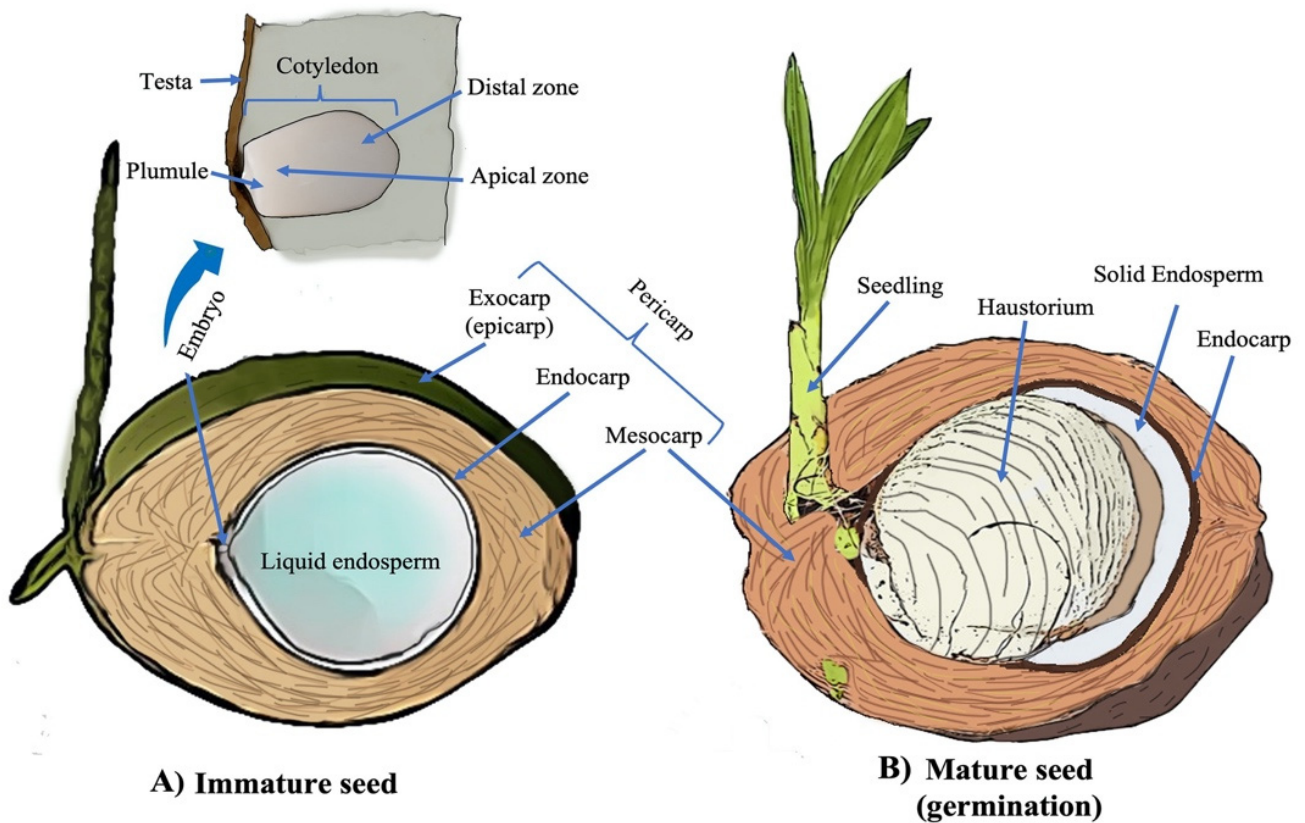


Figure 1. Structure of the coconut fruit and its components. (A) longitudinal section of the immature fruit; above, close-up of the embryo and (B) longitudinal section of the mature fruit in the process of germination.

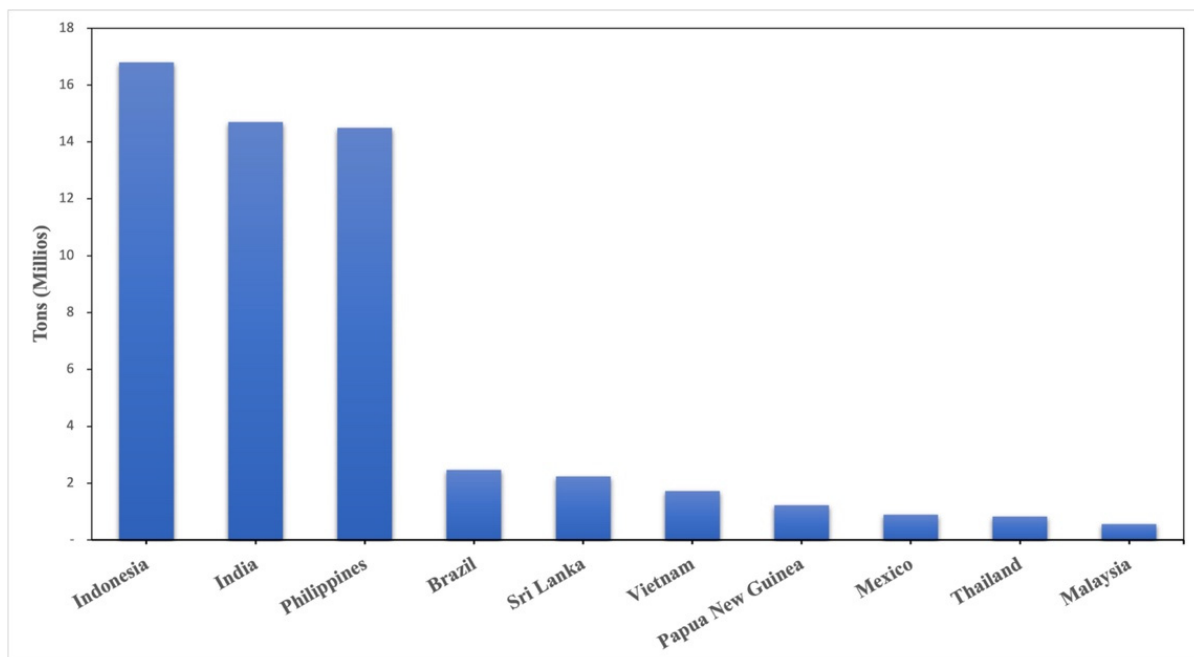


Figure 2. Main coconut producing countries in the world (preparation based on data from FAO, 2022).

The use of this species is compromised due to phytosanitary problems. In this work, a review of the most important diseases and pests of the coconut palm is presented, along with the emerging technologies based on “omics” and artificial intelligence used to

study the coconut palm-pathogen/pest interaction. Emphasis is placed on recent reports which begin to transcend the boundaries of the laboratory, towards the application of this information in pest and disease management.

2. Coconut Pests and Diseases

(a) Pests

Coconut palm is attacked by more than 900 species of insect pests, among those rhinoceros beetle, *Oryctes rhinoceros* L. (Coleoptera: Scarabaeidae), red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), coconut mite, *Aceria guerreronis* Keifer (Trombidiformes: Eriophyidae), and coconut black headed caterpillar, *Opisina arenosella* Walker Syn., *Nephantis serinopa* Meyrick (Lepidoptera: Oecophoridae), are the four major insect pests.

The “coconut fruit scab”, caused by the mite, *A. guerreronis* (Keifer) (Trombidiformes: Eriophyidae), is one of the most well-known. The mite settles on the fruit forming a whitish spot that spreads and turns brown; the damaged area becomes cracked and fibrous. If the fruit reaches physiological maturity, it is smaller and has less endosperm than a healthy fruit. There is no adequate biological control for this pest, and its chemical control, although acceptable, has severe effects on the environment [10]. This pest has been established in West Africa, Brazil, Mexico, the Philippines, and Indonesia, where it decreases 12–20% of fruit production [10]. The red palm mite *Raoiella indica* Hirst (Acari: Tenuipalpidae) is another great threat to the coconut palm. This is a gregarious species forming colonies that live and feed on the coconut abaxial leaf surface. Today, *R. indica* is distributed in all tropical areas of the Americas, as well as Brazil, where *R. indica* can cause a significant reduction in coconut yield, particularly when temperature and precipitation increase [11,12].

Another important pest in *Cocos nucifera* is the coconut palm weevil, *Rhynchophorus vulneratus* Panzer (Coleoptera: Curculionidae), a beetle that destroys more than 80% of susceptible coconut trees. Infection begins when the female oviposits on young leaves. The resulting larvae pierce the trunk or apical meristem (bud), forming tunnels that weaken and ultimately kill the plant. This weevil is found in Central and South America, India and Africa [10]. Alternative hosts for *R. vulneratus* are oil palm (*Elaeis guineensis*), finger palm (*Phoenix dactylifera*), sugar cane (*Saccharum officinarum*) and pineapple (*Ananas comosus*). *R. vulneratus* is a global threat and one of the biggest challenges for the coconut processing industry. In South America and Brazil, the weevil has been able to reduce the amount of copra destined to produce oil and other by-products [13]. Its biological control is complex. In contrast, cultural control (elimination of diseased palms and weeds), in combination with chemical control, is efficient in killing the larvae but it reduces the number of coconut plants and contaminates soil and aquifers.

The beetle, *Aspidiotus destructor* (Hemiptera: Diaspididae), known as the coconut scale, causes the disorder known as “coconut shell” which decreases fruit production. The female lays her eggs on the leaves, and upon hatching, the larvae attach and become covered by a whitish waxy coating and initiate sap sucking [14]. When infestation is high, mature and old leaves are the most damaged and fruiting is scarce. The insect is found in tropical and subtropical regions of the world and its alternative hosts are oil palm, mango (*Mangifera indica*), banana (*Musa* spp) and cacao (*Theobroma cacao*). The control of this pest is biological, using the species *Azya trinitates* (Coleoptera: Coccinellidae) and *Pentilia castanea* (Coleoptera: Coccinellidae), since chemical control, although it exists, is very expensive.

Another beetle that plagues the coconut palm is the rhinoceros beetle, *O. rhinoceros* L., which lays its eggs in the residue of dead palms in plantations. Once the larvae hatch, the young and adults fly towards neighboring coconut palms and enter the apical meristem, generating secondary infections and rupture of the crown [15]. Some alternative hosts are banana, sugar cane and papaya (*Carica papaya*). The beetle predominates in Asia and the South Pacific. The control of this pest involves a combination of biological control using *Metarrhizium anisopliae*, and cultural control through the elimination of decomposing organic matter. Chemical control is only recommended for short periods when the infesta-

tion is very severe. Recently, Izaitul et al. [16], reported that the hybrid cross of the Red Malayan Dwarf and Tagnanan shows tolerance to this beetle and produces large fruits with a thick copra.

Another phytosanitary problem in coconut is that of the beetle, *Xyleborus ferrugineus* L. (Coleoptera: Curculionidae), which makes galleries in the stems of plants and generally kills them. The adult females dig tunnels in the periphery of the trunk, feed on the wood and lay eggs in the deep parts of the cavities. The adults emerge from the galleries and colonize other plants. Its alternative hosts are cocoa and mango. Biological control is carried out with *Tetrastichus xilebororum* (Hymenoptera: Eulophidae), while cultural control is done by pruning and burning damaged parts. Chemical control is not very efficient since the larvae live inside the stem.

The black-headed caterpillar, *O. arenosella* Walker Syn., *N. serinopa* Meyrick is the most destructive defoliating pest of the coconut palm. The pest develops on the lower leaves where the caterpillar feeds on the sap. Chemical management is carried out by direct injection of insecticides in the stem; however, the accumulation of these compounds in the fruits limits their commercialization. The use of traps with the sexual pheromone (Z,Z,Z)-3,6,9-Tricosatriene, produced by the females of *O. arenosella*, is an eco-friendly strategy to which much attention has been paid. Although this strategy is efficient, sometimes its usefulness varies depending on environmental conditions [17]. The caterpillar can also feed on alternative hosts such as fan palms, wild date palms and date palms.

(b) Diseases

Diseases caused by oomycetes, phytoplasmas and fungi, are other constraints impacting the coconut palm. The bud rot disease (BPD), caused by the hemibiotrophic oomycete *Phytophthora palmivora* (Butler), causes enormous economic losses. BPD is characterized by the yellowing of young leaves, flag leaf rot, and bud rot of palm [18], but it is not easy to identify in the early stages. *P. palmivora* is a cosmopolitan organism, distributed in tropical and temperate climate regions with high levels of rainfall where the pathogen is more active in the wetter and warmer seasons of the year [19]. The oomycete affects nearly two hundred species of plants, in addition to the coconut tree, causing significant economic losses each year [18].

Another devastating disease is lethal yellowing of coconut trees (LYC), caused by phytoplasmas of the types 16SrIV-A, 16SrIV-D or 16SrIV-E, among others, and which has decimated natural populations and plantations throughout the world [20]. In Mexico, the initial impact of the disease reduced ~30,000 hectares of the cultivated area [21,22].

In Brazil, the fungus *Lasiodiplodia theobromae* is an important pathogen, that causes leaf blight disease. The pathogen invades the rachis to the petiole of the coconut palm, causing necrosis accompanied by gum liberation, which drives early defoliation and loss of bunches, leading to an important loss of coconut fruit yield [23]. This pathogen is widely distributed in India, and it is associated with the postharvest nut rot of coconut [24]. The basal parts of the fruits crack and become black, and water oozing may occur as the infection progresses. The pathogen enters the kernel, provoking a decay of the endosperm. The nuts become desiccated, shrunken, deformed and dropped prematurely. In the leaves, this pathogen causes the disease "leaf blight", drying leaves from tip downwards, inducing a charred or burnt appearance, more evident on lower fronds [25]. *Lasiodiplodia theobromae* causes significant monetary losses in the coconut industry in India.

3. Control Methods of Pests and Diseases in Coconut Crop

The top coconut producing countries are Indonesia, India, Philippines and Brazil, where the coconut crop is important for the economy, as well as social and cultural life. Coconut production is constantly threatened by phytosanitary problems. The following paragraph describes the control methods being used by the top producers to combat the coconut pest and disease problems.

(a) Chemical control

Chemical control is the most prevalent method used to control diseases and pests affecting coconut palms, but it presents a serious challenge to the environment, and the health of insects, animals and humans. Chemical control can also generate resistance within the pests which may further result in secondary outbreaks [12]. The black-headed caterpillar, *O. arenosella* Walker, and the red palm weevil, *R. ferrugineus*, are controlled using chlorpyrifos 20EC. *R. ferrugineus* is controlled with a mixture of dimethoate 30EC and Carbaryl 50WP; the emulsion is injected into the holes made by the red palm weevil, then sealed with mud or clay. Regarding the coconut scale, *Aspidiotus destructor* Signoret, Malathion 50Ec is the chemical of choice, while the mite *A. guerreronis* is controlled by applying monocrotophos 26WSC to the root of palms.

In case of bud rot disease (*P. palmivora*), a paste is prepared with 100 g of copper sulphate and 100 g quick lime, in 1 L of water (solution of Bordeaux) which is spread on the crown of the palms at the initial stage of the disease. Metalaxyl, phosphonates, or copper hydroxide can be applied with a brush to the cankers, while phosphonates can also be used as a systemic treatment applied in a soil drench, foliar spray or through trunk injection [19].

Recently Ushamalani et al. [26] evaluated fifteen different fungicides against *L. theobromae* under in vitro and in vivo conditions. Three chemical tests were found to be effective in vitro: carbendazim 50% WP, propiconazole 25% EC and tebuconazole 50% + trifloxystrobin 25% WG, but only carbendazim 50%WP works in the field, reducing disease by up to 20%. The result is not an optimistic one since the rate of reduction is low, and many fungi have become rapidly resistant to carbendazim [27–29].

Early attempts to control LYC involved the use of antibiotics such as oxytetracycline injected directly into the coconut trunk or petiole. These attempts were ineffective at arresting phytoplasma development and palms eventually died [30]. Unfortunately, an efficient method to control LYC does not currently exist.

(b) Biological control

The use of natural enemies is a cost-effective and ecofriendly strategy to control phytosanitary problems. In coconut, biological control has focused principally on the control of pests. The *O. rhinoceros* outbreaks in coconut farms may be controlled by the entomopathogenic fungus *Metarhizium anisopliae*. Mycosis is 100% effective in vitro; *M. anisopliae* penetrates the cuticle and mummifies the larvae. Since *O. rhinoceros* breeds in decomposing organic material, the inoculation of spores of *M. anisopliae* in coconut leaf vermicomposting sites was tested in India, finding a 72% reduction of *O. rhinoceros* larvae [31].

Huger [32] discovered a viral antagonist of *O. rhinoceros*, the *Oryctes rhinoceros* nucleopolydnavirus Huger (OrNV; formerly *Rhabdovirus oryctes* and *Baculovirus oryctes*). The release of 10–15 baculovirus-inoculated beetles per hectare was able to disseminate the virus in the pest population; OrNV enters the pest's body through oral ingestion and multiplies in the intestine, decreasing the pest population 15–20 days after ingestion. OrNV has been able to prevent outbreaks in the Pacific islands for more than 30 years [33]. However, between 2007 and 2015, a new haplotype of *O. rhinoceros* was identified in Guam, Port Moresby, Papua New Guinea, O'ahu, Hawai'i and Honiara, Solomon Islands; this new haplotype cannot be controlled with OrNV [34], evidencing the necessity of continuous monitoring and investigations into new control methods.

In Brazil, attempts are being made to control *R. indica* with the predatory lacewing *Ceraeochrysa caligata* (Neuroptera: Chrysopidae). The second instar of *C. caligata* has the ability to feed upon eggs and immature stages of *R. indica*, and may be a viable biocontrol agent against the red palm mite [12].

Regarding the red palm weevil, *R. ferrugineus*, entomopathogenic nematodes effectively control different developmental stages of the weevil. In Malaysia, the weevil is controlled with local isolates of antagonistic microorganisms such as the nematode *Steinernema* sp. That infects larvae and adults, and the predatory bird, *Dendrocitta vagabunda parvula* [35]. Recently, Rehman and Mamoon-Ur-Rashid [36] evaluated the entomopathogenic nematodes *Steinernema feltiae*, *Steinernema glaseri*, *Steinernema carpocapsae* and *Heterorhabditis bacteriophora*, against larvae, pupae, and adult stages of the red palm

weevil, in vitro and in field conditions. The four nematodes were highly pathogenic against larvae, followed by adult weevils, but their effect was minimal against the pupal stage. Under field conditions, the *S. carpocapsae* was the most virulent, causing 83.60% mortality of *R. ferrugineus*.

Biological control is also a key factor in the management of *Aspidiotus rigidus* Reyne (Hemiptera: Diaspididae). In the Philippines, multiple outbreaks of *A. rigidus* occurred from 2010 to 2016, and between 2017 and 2020 in the Zamboanga Peninsula, Mindanao Island [37]. Searching for biocontrol alternatives, the parasitoid *Comperiella calauanica* (Hymenoptera: Encyrtidae) was identified [37]. Recently, Almarinez et al. [14] evaluated the role of *C. calauanica* in the management of the outbreaks of *A. rigidus* in the areas where it was previously released for biological control. They found a high degree of parasitization by *C. calauanica*, which resulted in the prevention of outbreaks during two years after the release of the biocontrol insect, followed by infested coconut palms during the third year. Similar results were observed in different areas where the parasitoid *C. calauanica* was released, evidencing that biological control is important in the management of *A. rigidus*, but the biological control agent must be established and maintained to deal with a new invasion of *A. rigidus*.

(c) Integrated diseases and pest management of coconut crop

Most phytopathologists agree that the best options to deal with pathogens and pests are integrated management programs as they combine cultural control, biological control, biotechnology, and also the rational use of chemicals as a last resort. Integrated management usually involves the use (if possible) of resistant cultivars, pruning and good sanitation practices, and increasing organic matter in the soil to maintain a good fertilization regime [19,38]. Eradication of diseased or infested, or suspicious coconut palms is a common cultural control practice, especially for diseases such as LYC and BPD for which there are not effective control methods [19,20]. Other practices must be included to reinforce this practice such as farm quarantine, strict weekly surveillance, and burning of palms after cutting. When replanting, if possible, high yielding varieties and those with LYD and BPD resistance should be selected [20].

Suitable cultural control involves felling infected palms as well as surrounding palms that may not yet be infected or are asymptomatic. The destruction of coconut plants is also carried out in the control of the pests *O. arenosella*, *O. rhinoceros*, *R. ferrugineus* and sometimes *A. destructor*, which in main coconut producing countries such as India and the Philippines, means significant losses in the number of plants and production [38,39]. This agronomic practice also has a negative effect on the environment and climate because the practice of burning returns CO₂ to the atmosphere, while the reduction of plant biomass decreases its ability to absorb CO₂ from the air.

4. Omics and Its Application to the Study of the Coconut Palm

4.1. Genomics

Lantican et al. [40] sequenced the genome of the coconut palm, the dwarf variety “Catigan Green Dwarf” (CATD), using the PacBio SMRT platform. Although the authors obtained good quality information, the initial coverage was low (15×). The genome was then sequenced again using the MiSeq-Illumina platform where a depth of 50× was achieved. The assembled information estimated the size of the coconut palm genome at 2.1 gigabase pairs (Gbp), with a total of 34,958 genes [40]. Genes associated with economically important traits such as fatty acid biosynthesis (1-acyl-sn-glycerol-3-phosphate acyltransferase (LPAAT), phospholipase D, acetyl-CoA carboxylase carboxyltransferase beta subunit, 3-hydroxyisobutyryl-CoA hydrolase-like and pyruvate dehydrogenase E1 β subunit), and drought tolerance (213 drought-related gene homologs, among them ATP-binding cassette (ABC) transporters, abscisic acid (ABA) importers, and other genes involved in the uptake of the phytohormone abscisic acid) were identified. In the case of genes for resistance to pests and diseases, 340 resistance gene analogs (RGA) were identified which belong to 6 classes: (1) 90 genes encoding for CC-NBS-LRR (CNL) proteins; (2) 16 genes encoding

for CC-NBS (CN) proteins; (3) 2 genes encoding for TIR-NBS (TN) proteins; (4) 34 genes encoding for NBS-LRR (NL) proteins; (5) 5 genes encoding for TIR-unknown domain (TX) proteins; and (6), the largest class, with 192 genes encoding NBS-containing and transmembrane-coiled coil (TM-CC) domain-containing proteins. However, QTL mapping or functional analyses to correlate specific RGAs to specific diseases are necessary to enable the use of these genes for coconut breeding.

More recently, Yang et al. [41] sequenced the genome of a hybrid variety resulting from the cross of a Malayan yellow dwarf and a West African tall dwarf. The information was assembled at the chromosome level and compared with the oil palm genome, identifying large syntenic blocks that cover most of their genomes [41]. The assembled coconut genome is a very important tool to guide and interpret the results of current and further transcriptomic, proteomic and metabolomic studies in coconut.

4.2. Transcriptomics

The first coconut-related transcriptome was carried out by Verma et al. [42], analyzing the coconut root wilt disease. In infected plants, an increase in the presence of transcripts related to pathogenesis proteins (PRs) such as thaumatin, peroxidases, chitinases and glucanases was observed. Particularly noteworthy is PTI5, a transcript that encodes a transcriptional activator similar to the AvrPto avirulence protein of *Pseudomonas syringae*.

More recently, Gangaraj and Rajesh [18] analyzed the transcriptomes of the interaction between *C. nucifera* and *P. palmivora* at 0, 12, 24 and 36 h after infection. During the interaction, a total of 81,683 transcripts from the coconut palm and 9340 from *P. palmivora* were identified. Of that total, 64,639 transcripts from coconut and 9168 from *P. palmivora* were annotated, contributing to the understanding that *P. palmivora* pathogenesis and the coconut defense response are very complex processes. This information is available at <https://www.ncbi.nlm.nih.gov/sra/PRJNA544637>, accessed 11 December 2022, and represents a valuable database to identify targets to develop control methods against this pathogen in the coconut crop.

Another study of interest for coconut cultivation is the transcriptome derived from the *O. rhinoceros* beetle; Shelomi et al. [15] analyzed the intestine of the larva of this beetle in the instar (third) stage. Transcripts corresponding to the beetle microbiota were found, such as β -1,4-endoglucanases and cellobiases, highly homologous to those from termites, consistent with the fact that both species feed on wood. These novel results showed that those responsible for the degradation of the coconut cell wall are the microorganisms of the intestine of the beetle larvae. This can guide the implementation of measures against *O. rhinoceros* infestations, for example, by inhibiting these hydrolases.

On the other hand, Xu et al. [43] reported the transcriptomes of twelve stages of development of *O. arenosella*, the defoliating pest of coconut palms, whose risk is currently increasing due to climate change and the mobilization of infected material by human activity. The total number of transcripts was 41,938, of which 36,925 transcripts were recorded in public databases. Significant differential expression of many genes was found corresponding to their stages of maturation. The most expressed genes were related to growth and development, such is the case of ko04310, involved in signaling; Wnt, which regulates axial elongation, and ko04330, involved in the hormone-dependent signal transduction pathway determining the tissue pattern of nymphs [43]. The information from the transcriptome of this beetle is relevant to identify genes as those mentioned here, which may be targeted for its control. Double strand interfering RNA (dsRNAi) is an option which can control pests through targeting genes identified from transcriptomics studies [44,45].

4.3. Proteomics

Proteomics is one of the most frequently used massive analysis strategies in studies related to the coconut palm [46–52]. Coconut proteomics began with analyses of a few proteins by ionic exchange chromatography, size exclusion chromatography, and affinity chromatography, coupled to SDS-PAGE or double dimension electrophoresis [50–52], and

most recently, the development of high throughput proteomics sequencing resulted in the massive identification of proteins. Yang et al. [46] conducted iTraQ quantitative mass spectrometry-based proteomics to compare the Hainan Tall, BenDi (BD) and Aromatic coconut, XiangShui (XS) varieties under cold stress; the latter is cold-sensitive compared to the former. Some of the top KEGG enriched pathways in both coconut varieties under cold stress were RNA transport, protein processing in endoplasmic reticulum, and pyruvate metabolism; and proteins involved in photosynthesis, propanoate metabolism, purine metabolism and phenylalanine metabolism increased in both varieties. The proteomics suggests that phenylpropanoids and derivatives from tyrosine increased in the cold tolerant variety, while in the cold-sensitive variety, these metabolites did not accumulate [46]. Interestingly, plant-pathogen interaction proteins such as ABC transporter C family member 14 (ABCC14) and lipid-transfer protein (B3A0N2) were observed in both varieties, meanwhile the hypersensitive-induced response protein (H6TNP3) was only up-regulated in the cold-tolerant variety [29]. H6TNP3 was previously reported in the proteome of *Halogeton glomeratus* [53], as well as in *Musa paradisiaca* under salt stress. This provides evidence of crosstalk between abiotic and biotic stresses in plants.

To date, there is no proteomic investigation published which focuses on a pathogen-coconut interaction. However, there are some reports on related plants, from which it is possible to learn and get valuable information about coconut. For example, Rasool et al. [54] analyzed the proteome of date palm leaves infested with red palm weevil, *R. ferrugineus*, comparing it with mechanically wounded leaves as control. Thirteen specific proteins were observed in beetle-infested leaves, including stress response proteins such as mitochondrial heat shock 70 kDa protein, heat shock protein 81-2, and Em protein H5; the ion transporter V-type proton ATPase catalytic subunit A; proteins involved in carbohydrate metabolism such as glucose-1-phosphate adenylyltransferase small subunit and cellulose synthase-like protein D4. Two homologs of resistant proteins were differentially expressed specifically in red palm weevil-infested date palm leaves: the putative late blight resistant protein R1B-8 (uniprot Q69QQ6) and putative late blight resistant protein RIA-10 (uniprot Q60CZ8). This study shows that proteomics can be used for phytosanitary diagnosis; these differential proteins may be used as early biomarkers to monitor infestation to prevent the spread of the weevil throughout the plantation and maybe even for the selection of resistant coconut varieties.

Rhynchophorus ferrugineus is a key pest not only for date palm but also for Arecaceae palms in general; in South and Southeast Asia this beetle is a key pest of coconut. In March 2017, The Food and Agriculture Organization (FAO) called for collaborative efforts at regional and global levels to combat this pest [55]. The search in the coconut genome for orthologs to uniprot Q69QQ6 and Q60CZ8 proteins is a promising beginning to find solutions against this beetle in coconut. Additionally, Yang et al. [56] recently conducted the transcriptome and gene expression analysis of pupa, 7th-instar larva, and adult stages of *R. ferrugineus*, finding 8583 differentially expressed genes, mainly involved in amino acid synthesis, metabolism, and organ tissue formation. Interestingly, the transcription factor (TF) families zf-C2H2, ZBTB, TF-bZIP were up-regulated in larvae and pupa; transcripts for serine hydrolases and peptidases were up-regulated in larvae too, consistent with the larvae's need to consume large amounts of proteins to satisfy their developmental needs. Since TFs regulate the growth, development and immunity in insects, and since proteases play key roles in larvae nutrition, they represent potential candidates that can be targeted for the control of *R. ferrugineus*.

4.4. Metabolomics

Interesting metabolomic studies exist that focus on volatile molecules which are powerful insect attractants. Regarding coconut pests, the aggregation pheromones of the *O. rhinoceros* beetle haplotype G, ethyl 4-methyloctanoate and 4-methyloctanoic acid were isolated in a metabolomics investigation [57]. Purification of this pheromone showed that only males produce the "R" enantiomer, the active compound, while females produce

the “S” enantiomer. The pure ethyl (R)-4-methyloctanoate compound was evaluated in the Solomon Islands and it was a success as a strong attractant for males and females of rhinoceros beetles [57]. This result is hopeful and opens the possibility of using this metabolomic strategy to search for biological control methods against other coconut pests.

Recently, Ding et al. [58] performed a transcriptomic study on the reproductive glands of the moth, *Euphestia (Cadra) cautella* Walker (Lepidoptera: Pyralidae); this moth causes enormous losses on stored products of coconut, corn, wheat, chocolate, etc. In this work, three new enzymes were discovered, 12-carbon fatty acid desaturases, a fatty acid reductase and an acetyl transferase. The cDNAs of these three enzymes were co-expressed in the yeast *Saccharomyces cerevisiae*, and the metabolic product, (Z,E)-9,12-tetradecadienyl acetate (zeta pheromone) was detected. The zeta pheromone was found to be a powerful inducer for aggregation in this moth [58].

Table 1 shows a summary of the omics reports related to pathogens and pests causing important phytosanitary problems in coconut palms.

Table 1. Targetable genes in coconut or its pathogens/pests identified by omics approaches.

Study	Organism	Targetable Genes	Functions	Observations	Reference
Genomics of coconut	Coconut	Resistance gene analogs (RGA)	Resistance to pests and diseases	The identification of particular RGAs for resistance to specific pathogens and pests is necessary	[40]
Transcriptomics of root wilt disease of coconut (causal agent phytoplasma)	Coconut	NBS-LRR domain proteins	Signal transduction to induce the plant defense against pathogen attack	Up-regulated	[42]
Transcriptomics of root wilt disease of coconut (causal agent phytoplasma)	Coconut	PR1, PR4	pathogenesis-related proteins	Supports the defense mechanism against RWD	[42]
Transcriptomics of root wilt disease of coconut (causal agent phytoplasma)	Coconut	PTI5-like gene	pathogenesis-related genes transcriptional activator	Highly up-regulated	[42]
Transcriptomics of root wilt disease of coconut (causal agent phytoplasma)	Coconut	HSP70	A chaperone involved in hypersensitive response in plant defense mechanism	Highly up-regulated	[42]
Transcriptomics of <i>C. nucifera</i> and <i>Phytophthora palmivora</i> interaction	Coconut	64,639 coconut transcripts	–	Draft of dataset. Needs to be characterized to identify targetable genes	[18]
Transcriptomics of <i>C. nucifera</i> and <i>Phytophthora palmivora</i> interaction	<i>P. palmivora</i>	9168 <i>P. palmivora</i> transcripts	–	Draft of dataset. Needs to be characterized to identify targetable genes	[18]
Transcriptome of the beetle <i>Oryctes rhinoceros</i>	<i>O. rhinoceros</i>	β -1,4-endoglucanases and cellobiases	Degradation of the coconut cell wall. Feeding	Up-regulated in the intestine of the beetle larvae	[15]

Table 1. Cont.

Study	Organism	Targetable Genes	Functions	Observations	Reference
Transcriptome of the moth, <i>Euphestia (Cadra) cautella</i>		The genes codifying 2-carbon fatty acid desaturase, fatty acid reductase and acetyl transferase	Involved in the biosynthesis of the pheromone (Z,E)-9,12-tetradecadienyl acetate	Power pheromone that induces aggregation in this moth. Its production is by heterologous expression of the three enzymes.	[58]
Transcriptome of <i>Rhynchophorus ferrugineus</i>	<i>R. ferrugineus</i> (red palm weevil)	zf-C2H2, ZBTB, TF-bZIP transcription factors	Regulate growth, development and immunity in insects	Up-regulated in larvae and pupa stages	[56]
Transcriptome of <i>R. ferrugineus</i>	<i>R. ferrugineus</i> (red palm weevil)	serine hydrolases and peptidases	Proteases with role in feeding	Up-regulated in larvae stage	[56]
Proteomics of interaction of date palm leaves (close coconut relative) and <i>R. ferrugineus</i>	Date palm	homologs to the late blight resistant protein R1B-8 and late blight resistant protein RIA-10	Up-regulated in date palm infested with this red palm weevil	Identification of orthologs of these RGAs is necessary in coconut as well as the elucidation of its role in red palm weevil infestation	[54]
Metabolomics studies of the beetle <i>Oryctes rhinoceros</i> , haplotype G	<i>O. rhinoceros</i> ,	The pheromone ethyl (R)-4-methyloctanoate	The “R” enantiomer is a strong attractant for males and females of rhinoceros beetles	Genes involved in (R)-4-methyloctanoate biosynthesis need to be identified for further production of this pheromone by genetic engineering	[57]
Metagenomics identification of mycorrhizal fungi associated with coconut roots	Coconut	Species of <i>Glomus</i> , <i>Sclerocystis</i> , <i>Rhizophagus</i> , <i>Redeckera</i> , and <i>Diversispora</i> genera	Mycorrhizal fungi improve nutrient uptake from the soil and modulate plant defenses against insects and pathogens.	These were the most abundant species associated with coconut roots	[59]

5. Opportunities and Challenges Going forward: From Omics-Based Results to Solutions for Phytosanitary Problems in the Coconut Palm

Since omics studies generate large amounts of information, the number of resulting potential targets may be high. The two main paths that exist involve targeting genes from the host or targeting genes in the pathogens or pests.

With respect to coconut palms, some targetable genes comprise the resistance-like kinase (RLK) genes overexpressed in coconut plants with root wilt disease [42]), or the resistance proteins differentially expressed specifically in coconut leaves infested with red palm weevil. These sequences could be targeted for disease control using strategies such as CRISPR/Cas9 editing or cisgenesis.

However, the genomic edition of tropical crops is challenging. Some bottlenecks have been solved, such as the establishment of tissue culture procedures [60], but it is necessary to improve the transformation of the coconut crop. Currently, there is a single report on the transformation of embryogenic calli by *Agrobacterium tumefaciens* in combination with biobalistics, but transformation was transient [60]. It is necessary to achieve stable transformation to be capable of targeting genes in this crop.

As an alternative, the identified genes may be used in molecular markers-based genetic improvement programs. That strategy has been successfully used for other crops. For example, the genome of potato (*Solanum tuberosum* L.) was the center of a study that identified genes that share homology with those found within the Pathogen–Host

Interactions database, and QTLs were constructed and identified in the genome. The inheritance of the QTLs for resistance to potato dry rot caused by *Fusarium sambucinum* was analyzed, revealing that the most reproducible QTL for this trait was mapped on chromosome I of potato. In other works, the breeding programs of potato have been based on *Rpi* genes (for resistance to *Phytophthora infestans*). One of these programs, Bioimpuls, an 11-year-long project, achieved the introduction of multiple *Rpi* genes such as *Rpi-cap1*, *Rpi-chc1*, *Rpi-vnt1* and *Rpi-blb2*, among others, into susceptible potato cultivars [61]. Like potato, coconut requires long breeding cycles since sexual maturity is reached from 3 to 6 years after field planting, and the fruits need to be observed for several years [62], so, lengthy projects are necessary for these goals.

It is probably easier to target genes in pathogens and pests, and the most promising technique involves silencing with RNAi, especially by spray technology. Currently, RNAi constructs may be constantly expressed in plant tissue, a procedure known as host-induced-gene-silencing (HIGS), or expressed transiently by using viral-based vectors, a procedure known as virus-induced-gene-silencing (VIGS). These two procedures, HIGS and VIGS, have been proven effective in the control of fungal pathogens and pests in other crops [63–65]. Both methods involve transgenesis or the production of genetically modified organisms (GMO); such organisms are rejected by the current legislation found in many countries. Spray-induced-gene-silencing (SIGS) does not involve the handling of GMOs, which makes SIGS the most attractive technology for targeting genes for crop protection. Sprayable RNAi-based products have been effective in controlling *Plutella xylostella* (Lepidoptera: Plutellidae) [66], *Ostrinia furnacalis* (Lepidoptera: Crambidae) [67] and *Diaphorina citri* (Hemiptera: Liviidae) [68], among others, with a degree of mortality between 42% and 89%. SIGS also works on aphids [69], but sprayable RNAi-based products need to be tested in each case since the penetration of RNAi through the cuticle varies among different insects. Absorption of RNAi by fungi is variable and less effective than in insects, but this strategy is currently being considered for the control of fungi and oomycetes [70–72]. Some of the challenges to be faced are the improvement of the stability of RNAi and RNAi absorption. Both areas are currently under intensive research, which allows us to be optimistic about the use of SIGS to control plant diseases in coming years.

Another promising option for pest control, although incipient, is the heterologous expression of enzymes involved in pheromone synthesis, such as (Z,Z,Z)-3,6,9-Tricosatriene, the sexual pheromone produced by the females of *O. arenosella* [17], the ethyl (R)-4-methyloctanoate, the aggregation pheromones of the *O. rhinoceros* beetle haplotype G [39], or the zeta pheromone, the aggregation pheromone of the moth *E. cautella* [58]. Many other gene clusters involved in the biosynthesis of pheromones may be identified from omics approaches for use in the control of coconut pests.

Other omics technologies may also contribute to the development of strategies to control diseases and pests in coconut. For example, Lara-Pérez et al. [59], through metagenomics, studied the diversity of mycorrhizal fungi associated with coconut roots, finding that the most abundant species belonged to the genera *Glomus*, *Sclerocystis*, *Rhizophagus*, *Redeckera*, and *Diversispora*. This presents an opportunity to build consortia of these mycorrhizal fungi to promote sustainable agriculture for the improvement of nutrition as well as biotic and abiotic stress tolerance during coconut cultivation since mycorrhizal fungi improve nutrient uptake from the soil and modulate plant defenses against insects and pathogens [73,74].

6. Discussion

The coconut tree is a subsistence crop for small and medium-scale producers in the world. The challenges and uncertainties that pathogens pose threaten to extinguish the crop. For example, in the Solomon Islands and Vanuatu in 2018, the *O. rhinoceros* beetle haplotype G, insensitive to the control pheromones available at the time, severely damaged the coconut and oil palm industry that was valued at 38 million dollars [75]. The following

year, production in Indonesia, the Philippines and India, the three largest global coconut producers, was decimated by ~15% due to pests and pathogens [76].

Control strategies that deal with pathogens and pests in coconut crops are principally chemical control, biocontrol, cultural practices and integrated management strategies. Chemical control is the most prevalent method, but among its inconveniences are the contamination of environment and rapid development of resistance in pathogens and pests, as the case of carbendazim, a fungicide in the chemical group of benzimidazols, identified as the most effective fungicide against *L. theobromae* [26]. Therefore, efficacy against this pathogen is expected to be short-lived. Furthermore, no chemical product is effective so far against *P. palmivora* (causal agent of BPD), 16SrIV (A-D) phytoplasmas (causal agent of YLC), or the pest *Raoiella indica* Hirst, among others, making their control even more challenging.

The antibiotic, oxytetracycline, is still injected into the cabbage palm trunk to arrest the phytoplasma [77], although the early report found poor results in the coconut palm [30]. In cabbage palm, oxytetracycline was able to prevent infection on treated healthy palms, but early symptomatic palms that were treated showed similar levels of phytoplasma to the control group [78], reinforcing that effectiveness of oxytetracycline on phytoplasmas is low.

Hollomon [79] investigated the susceptibility of *Aspergillus fumigatus*, a fungal human pathogen, to azole fungicides used in human medicine (Itraconazole, Voriconazole, Posaconazole) and in agriculture (Propiconazole, Difenoconazole, Epoxiconazole, Bromuconazole, Tebuconazole). Strains were isolated from clinics and from the environment, and it was found that all strains were resistant to all azole fungicides, even those with which the fungi had supposedly never come into contact. In addition, the same mutations in the Cyp51 gene (that codifies lanosterol 14 α -demethylase) were identified in the different strains, independently of their origin. These results evidence the risk in using molecules belonging to the same chemical group to control pathogens in medicine and agriculture. The antibiotic, oxytetracycline, used against phytoplasmas, is also used on a number of human pathogens that cause Chlamydia, cholera, typhus, anthrax, malaria, syphilis, respiratory infection, streptococcal infection, and acne [80]. Sharing this antibiotic with the agricultural sector may accelerate the emergence of oxytetracycline-resistant bacterial human pathogens.

One of the most frequent agricultural practices to control pathogens (e.g., *P. palmivora*, 16SrIV phytoplasmas) and pests (e.g., *O. arenosella*, *O. rhinoceros*, *R. ferrugineus*) of the coconut crop is the elimination of infected or infested plants. However, this task has an important economic impact on coconut growers due to the loss of a significant number of coconut plants, as well as the deleterious effect on the environment.

The “secrets” of the coconut palm, as well as its pathogens, are currently being revealed; these include genome and proteome information (Figure 3), as well as the identification of pheromones and the genes responsible for their synthesis [81]. Globally, phytosanitary problems have reduced the income of coconut palm producers by up to 50%, thereby necessitating the implementation of prevention and control measures [82].

The results of omics projects may help to find solutions to these recalcitrant phytosanitary problems. For example, pathogenicity and essential genes in insect pests are targetable for silencing by SIGS, which is probably the most promising biotechnological method to control insect pests.

Finding targetable genes in phytoplasmas is extremely challenging because they are obligated parasites that cannot be isolated. However, phytoplasmas are insect-transmitted, and those biological vectors may be subjected to SIGS. In addition, RNAi may be designed to specifically target a single organism, preventing off-targets, especially those of human pathogens.

Currently, one of the most remarkable post-genomics applications to control pests is the identification of biosynthetic pheromone clusters to produce pheromones using genetic engineering. This approach is a sustainable and effective method to control the caterpillar

O. arenosella, *O. rhinoceros* beetle haplotype G, and the moth *E. cautella*. This strategy is largely promising and should be exploited for control of other pests.

Regarding the coconut palm (host), it is necessary to improve genetic transformation to exploit genomics data by using CRISPR-Cas9 or cisgenesis. Likewise, the identification of omics data of QTLs associated with desirable traits may be the base for molecular marker-based breeding in coconut. Although this strategy requires a great investment of time, it is a feasible strategy for coconut palm.

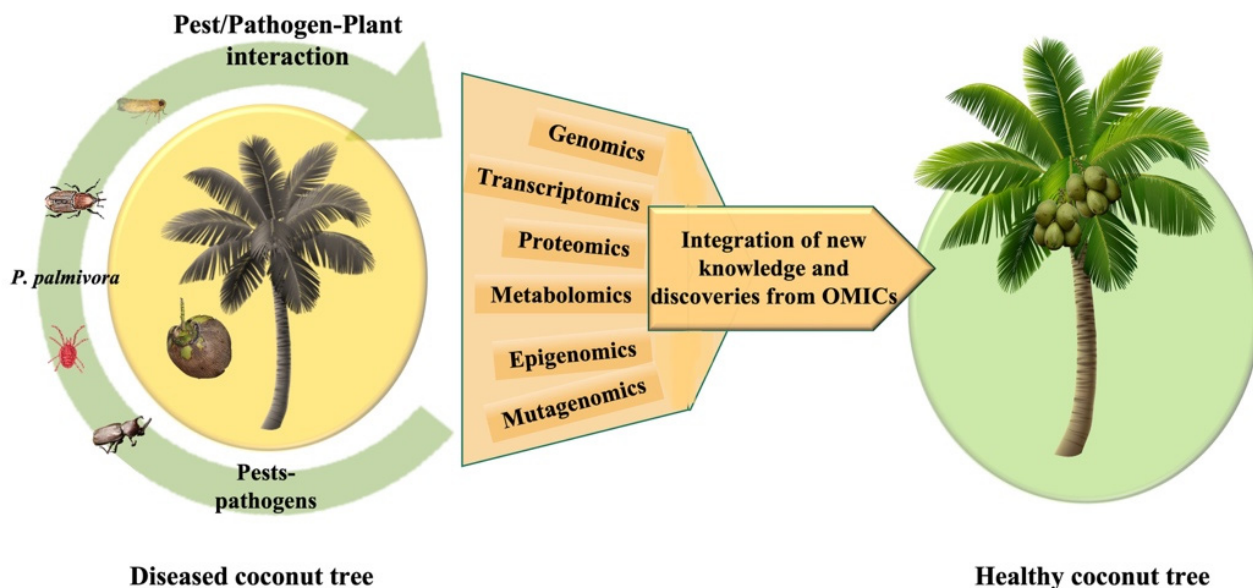


Figure 3. Schematic figure representing the contribution of the omics studies to our current understanding of the coconut and pathogen/insect interaction, as well as their contribution to the identification of novel strategies for pest and disease control.

The execution and application of “omics” research specific to the coconut palm is the strategic pivot needed to alleviate the problems of the industry. Advances in other disciplines, such as artificial intelligence, support this new paradigm. The creation and enrichment of biological databases and their mining can generate machine-learning patterns that allow for disease identification and diagnosis in animals and plants [83]. Recently, Alsanea et al. [84] developed a method for the instantaneous identification of the red palm weevil based on a deep-learning algorithm. The algorithm was fed with 300 images of different parts of the body of the red palm weevil where specific structures or “markers” are located; the algorithm identified this insect with an accuracy of 93–100%, even in palms in the early stages of infestation. The algorithm appears promising for the control of the red palm weevil, with added utility against other agricultural pests.

7. Conclusions

Massive analysis projects have and continue to yield a large amount of information that must be interpreted and integrated for biotechnological use. An increase in the detection of pests through artificial intelligence is anticipated, as well as the identification of biosynthetic pheromone clusters. This identification, together with genetic engineering and synthetic biology, allow for the realization of “omics” projects for pest control that are more efficient and eco-friendly.

Research approaches are increasingly more holistic, so in the future, other strategies will be incorporated in the search for solutions against coconut pests and diseases such as metagenomics, epigenomics and mutagenomics, among others. The induction of mutagenesis in in vitro cultures could facilitate the generation of large populations of mutagenized plants which can be maintained under controlled conditions, in limited spaces and at any time of the year. During this time, gene mutants with important traits for coconut plant

breeding, such as resistance to pests and diseases or increased production of medium chain fatty acids can be investigated. Technologies such as CRISPR-Casp9, RNAi and heterologous protein expression will be key allies to push omics results from the labs to control coconut palm diseases and pests in the field.

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