



Molecular shields of the palm: proteomic insights into biotic stress in arecaceae

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Abstract The Arecaceae family, comprising economically significant species such as coconut, oil palm, and date palm, has been central to human nutrition and agricultural development since early civilization. Economically, it is among the most vital plant families. Oil palm (*Elaeis guineensis*), for instance, is a vital source of edible oil, while date palm (*Phoenix dactylifera*) yields fruits with high nutritional value and is widely consumed. Researchers have been intrigued by the complicated behaviour of palm tree family members, aiming to identify noteworthy transcripts, proteins, or metabolites that may be connected to important traits. Proteomics, has greatly advanced

the knowledge of how plants function. Using different techniques, scientists have mapped proteins across various parts of the plant in different environments. Novel techniques such as gel-free shotgun LC–MS/MS proteomics are included in this review, along with a summary of the main proteins of interest that have been discussed and could be potential protein selection markers for crop improvement. Notable findings include identifying stress-related proteins like heat shock proteins and antioxidant enzymes, as well as proteins linked to stress responses and defence

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mechanisms, such as pathogenesis-related proteins in oil palm and date palm leaves. This review synthesizes the latest progress in Arecaceae proteomics and discusses prospective biomarkers that could support breeding more resilient cultivars. Insights from this review aim to support breeding efforts focused on enhancing stress tolerance and overall crop performance in Arecaceae species. The insights from this review may aid in the development of plants with enhanced stress resistance.

Keywords *Arecaceae* · Crop improvement · Molecular mechanisms · Palm proteomics

Introduction

The *Arecaceae*, also known as the palm family, are flowering plants known for their enormous and diverse morphological and environmental adaptation (Hoang et al. 2022). Approximately 2600 species in 181 genera are found throughout the world in various types of ecosystems, from rainforests to deserts (Yao et al. 2023). Their suitable adaptation and evolution, have significant economic implications in food production, biofuel, and horticulture (Chen et al. 2022). Their morphological diversity includes many growth types, from climbers to shrubs to large trees. Some species are distinctive because of their enormous size, others by their odd reproductive strategies, or their unusual morphologies.

Besides their ecological relevance, palms are plants of great economic importance. Many species of the *Arecaceae* family serve key roles in food production, horticulture, and biofuel generation. Oil palm (*Elaeis guineensis*), for example, is an excellent source of edible oil for use in cooking and food preparation (Chen et al. 2022). Another commercially significant palm is the date palm (*Phoenix dactylifera*) which is a delicious and healthful date consumed all over the world (Al-Karmadi and Okoh 2024). Additionally, palms have a role in the production of biofuels, with some species serving as a reliable supply of biomass for power production the coconut (*Cocos nucifera*), and the açai palm (*Euterpe oleracea*) (Abdelghaffar et al. 2023; Barcelos et al. 2015). Other species add significant value to the world economy by being appreciated for their lumber, foliage, or decorative plants (Sin 2015). Therefore, the development

of plants that can resist changing climatic conditions and feed an expanding population will be essential to ensuring that there will be enough food for the predicted 9 billion people by 2050 (Bitu and Gerats 2013). Plants have developed a variety of physiological and molecular defence mechanisms to deal with both abiotic and biotic stress circumstances since they are fixed organisms that cannot escape from changing environmental conditions (Ghatak et al. 2017; Al-Obaidi et al. 2024a). To accurately examine the quantitative and qualitative changes and consequences brought on by the relevant stress state, it is necessary to apply a systems biology method to identify genes, proteins, and biochemical compounds. The “omics” technology has advanced recently, yet researchers still struggle to find good correlations between the data collected on various platforms (Panahi et al. 2024). Because of transcript degradation and post-transcriptional regulatory processes, changes at the RNA expression level may not always translate into changes at the protein level (Nouaille et al. 2017). Proteomics and metabolomics research offer valuable insights into how genes and proteins respond to different stress conditions, helping us understand complex stress responses (Hu et al. 2015; Nakabayashi and Saito 2015). Research at both the genomic and transcriptome levels has been intensively carried out over the last few years on the members of the *Arecaceae* plant family to increase our understanding of their remarkable diversity and resilience (Al-Obaidi et al. 2016a; Andrade et al. 2020; Anishkumar et al. 2022; Ibrahim et al. 2023; Khanum et al. 2023; Caro et al. 2022; Chu et al. 2023; Pammit et al. 2022; Sabana et al. 2022; Darnet et al. 2023; Francisconi et al. 2022; Neto et al. 2023). These investigations increased our understanding of the biology of the palm family, but they only provide us with a fragmentary picture of how the organism functions. The fundamental agents of biological function, proteins, hold the solutions to numerous unrecognised features of *Arecaceae* biology. Proteomics, genomics, and transcriptomics may all be used together to help researchers grasp biological processes more thoroughly. Studying genes, RNA, and proteins together can give a fuller picture of plant biology and how different layers of cellular information interact. As a result, our knowledge of biological processes and their regulation is expanded (Depuydt et al. 2022).

Researchers may get an inclusive view of the proteins involved in certain biological processes, signalling pathways, or disease situations thanks to this comprehensive examination (Lau et al. 2018). Proteomics allows us to examine the whole collection of proteins encoded by a genome, including their modifications, relationships, and functional activity, providing a more dynamic and functional snapshot of an organism's biological status than genomics alone (Al-Obaidi et al. 2024b). Proteomic research could provide insight into the molecular mechanisms underpinning the distinctive morphological characteristics, varied physiological functions, responses to

environmental challenges, and disease resistance of the *Arecaceae* family (Zhou et al. 2022). Additionally, the knowledge gained from these investigations could be extremely helpful in enhancing the production and quality of commercial products made from palm. Proteomics could vastly enhance our understanding of several critical areas, including the distinctive morphological traits, physiological processes, reactions to environmental challenges, and disease resistance mechanisms, in the context of the *Arecaceae* family (Yan et al. 2022). Although proteome analyses of *Arecaceae* species have the potential to reveal extensive information (Fig. 1), this field is yet

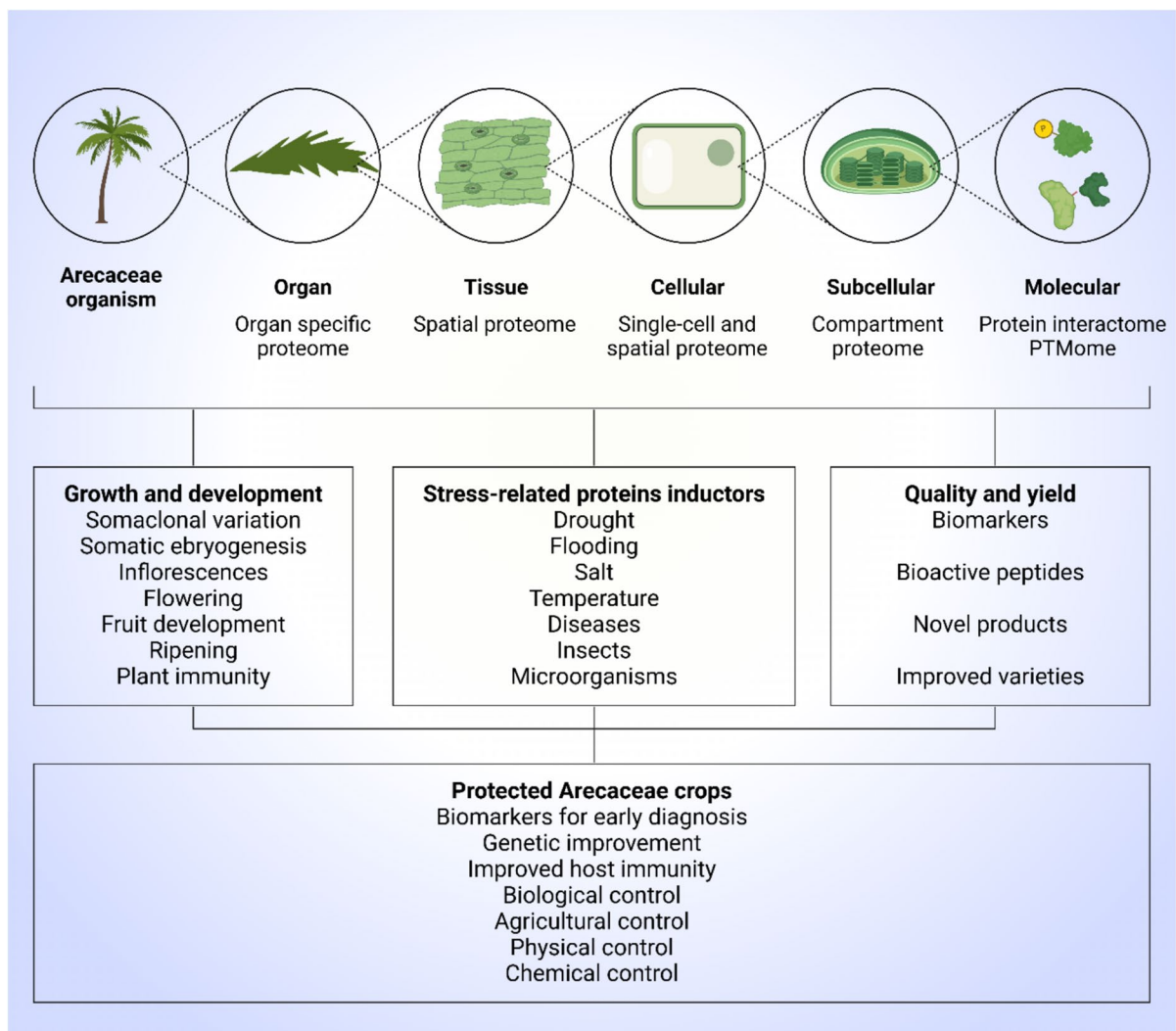


Fig. 1 An overview of the proteomic research, carried out in *Arecaceae* family

mostly under-explored. While a few research have concentrated on particular palm plants like date palm (*Phoenix dactylifera*), coconut (*Cocos nucifera*), and oil palm (*Elaeis guineensis*), the *Arecaceae* family's general biological diversity has yet to be thoroughly studied by proteomics analysis (Depuydt et al. 2022). The entire range of the *Arecaceae*'s biological diversity has not yet been covered by an in-depth, family-wide proteome analysis.

The results from proteomic research within the *Arecaceae* family represents an important resource of information to uncover essential proteins related to stress tolerance. Proteins participating in antioxidant pathways like catalase (CAT), and peroxidases (POD) are crucial for scavenging reactive oxygen species [ROS], levels of which are typically increased under different types of abiotic stresses, such as drought or salinity. Moreover, proteins connected to hormonal regulation (in particular abscisic acid [ABA] signalling) (Alrajeh et al. 2024), render genotypes less susceptible to stress and so could serve as messengers for the selection of resistant cultivars. Breeders and genetic engineers can use these analyses to help develop *Arecaceae* cultivars that can survive environmental stresses ranging from extreme conditions (drought, salt stress) down to pathogen attacks as well as nutrient limitations.

In the sago palm (*Metroxylon sagu*), adaptive responses to deep peat soil environments were marked by the upregulation of key proteins associated with photosynthesis and stress tolerance. Notably, ribulose biphosphate carboxylase/oxygenase activase and oxygen-evolving enhancer proteins were elevated, enhancing carbon fixation and photosystem stability, essential for maintaining photosynthetic efficiency under stress. Additionally, increased levels of carbonic anhydrase and glutamine synthetase supported improved carbon and nitrogen assimilation, respectively, while ascorbate peroxidase activity indicated enhanced oxidative stress protection. These proteins underline the sago palm's strategy of metabolic and photosynthetic adjustment in peat environments, potentially at the cost of normal trunk development, reflecting a unique adaptation among palm species to tolerate nutrient and water limitations (Hussain et al. 2020). Despite that, our knowledge of the diversity, abundance, and purpose of proteins in different palm species is still seriously lacking. As genetic and proteomic data becomes more abundant in the *Arecaceae*,

which is a family of unparalleled complexity at both levels, this leads to new resources applicable for research in breeding systems or functional genomics. ArecaceaeMDB is a specialized multi-omics database for palm trees, which contains the data of genomic research together with transcriptomic and proteomic as well as metabolomic information. It would serve as an important resource for genetic and protein markers identification supporting the development of stress-resilient cultivars in multiple palm species including coconut, oil palm, date palm, etc. Its utility comes from allowing access to different omics data for comparative research and functional analyses that enable targeted breeding or genetic modifications to develop more resilient and productive crops.

Proteomic response of *Arecaceae* plants to stress

All plants, including *Arecaceae* species, are susceptible to biotic stress caused by pathogens and pests. These biotic stresses can harm palm populations, resulting in lower crop yields and economic losses. Understanding the molecular responses of *Arecaceae* plants to biotic stresses is vital for developing effective conservation plans for these important species. Proteomic investigations have proven to be useful in unravelling the complex molecular processes underlying plant responses to biotic stresses. The key protein molecules and pathways involved in *Arecaceae* plants' defence mechanisms will be clarified by studying proteomic research on how they respond to biotic stresses (Ramli et al. 2020). Biotic stresses in *Arecaceae* plants include a diverse set of issues caused mainly by pathogens, pests, and herbivores. Some of the most frequent biotic stresses have an impact on palm species (Osman et al. 2023). Diseases caused by *Fusarium* spp., *Ganoderma* spp., and *Phytophthora* spp. can cause wilting, rotting, and even death in *Arecaceae* plants.

Proteomic investigations have revealed an array of pathogenesis-related (PR) proteins, including PR-1, PR-2, and PR-5, that increase in response to fungal pathogens in oil palms and date palms. These proteins are known for their role in reinforcing plant defence, suggesting that enhanced expression or selection of these proteins could improve biotic stress resistance in cultivated palm cultivars. Similarly, heat shock proteins (HSPs) and antioxidant enzymes like

superoxide dismutase (SOD), identified in coconut and date palms, are crucial for countering oxidative stress, which can occur under high-temperature and drought conditions. Targeting these proteins could aid in developing cultivars that are more resilient to environmental stresses by enhancing their ability to maintain cellular stability under adverse conditions. Proteomic research on *Arecaceae* plants exposed to biotic stresses showed a wide range of proteins involved in defence responses. Pathogenesis-related proteins (PR), glucanases, chitinases, and protein kinases are a few examples. PR proteins are well-known plant defence markers that play important roles in pathogen inhibition. Proteomic research has revealed substantial modifications in the activity of several proteins involved in defence responses. For example, research on oil palm (*Elaeis guineensis*) infected with the destructive fungal pathogen *Ganoderma boninense* revealed altered accumulation levels of enzymes associated with lignin biosynthesis and secondary metabolism (Al-Obaidi et al. 2017, 2010). *Arecaceae* plant biotic stress responses often involve complex hormone signalling pathways. Proteomic research has revealed details about the modulation of hormonal pathways such as jasmonic acid (JA), salicylic acid (SA), and ethylene (ET) in response to biotic stresses. These pathways regulate the expression of defence-related genes and proteins (Mishra et al. 2024). Plant defence mechanisms include reactive oxygen species (ROS) and antioxidant enzymes. Proteomic investigations have shown the importance of antioxidant enzymes like catalase (CAT), and peroxidase (POD) in scavenging ROS and preventing cellular damage during biotic stress (Fig. 2). In plants, the interaction of different proteins is critical for orchestrating defence responses (Garcia-Caparrós et al. 2021). Components of innate immunity, along with pathways related to hormone signalling, oxidative stress response, and pathogen-specific defence, provide specific markers that could be targeted to breed or select transgenic plants with enhanced resistance to both biotic and abiotic stressors.

The recent multi-omics study on date palm (*Phoenix dactylifera*) analyzed the plant's responses to high-salinity stress, equivalent to seawater exposure, focusing on both roots and leaves. This integrative approach revealed that date palms combine “avoidance” strategies, like reducing Na^+ and Cl^- uptake in roots, with “acclimation” responses, such as

enhancing antioxidant activity in leaves to manage reactive oxygen species. Key findings showed that salt tolerance in date palms involves changes in root transporter proteins that limit salt ion buildup, while leaves accumulate potassium to sustain cellular functions. Hormonal shifts, including transient ABA increases, aid in stress signalling, and a strengthened antioxidant response protects photosynthetic tissues. These insights highlight adaptive mechanisms that enable date palms to thrive in saline environments, with potential implications for improving crop resilience (Muhammad et al. 2024).

Fungal disease

Fungal diseases pose a threat to palm trees, including several palm trees. If left untreated, these diseases can cause serious damage to palm trees, resulting in reduced development, wilting, defoliation, and even death. Scientific research has looked at fungal endophytes and how they might improve the stress resistance and climatic adaptation of date palm plants in coastal dune ecosystems (Mahmoud et al. 2017). Notably, *Fusarium* and *Clonostachys* were the dominant genera, clearly distributed throughout all of the sample sites that were surveyed. *G. boninense* is considered one of the devastating species of oil palm tree, The plant responds in leaves (Al-Obaidi et al. 2016a; Jeffery Daim et al. 2015), roots (Al-Obaidi et al. 2016a) and trunk (Mostapha et al. 2018) to this pathogen has been well studied at the proteomic level. The findings from these investigations have shed light on defence-related proteins that are upregulated in oil palm tissues infected with *G. boninense*. PR-1, PR-2, PR-5, and PR-10 are examples of pathogenesis-related (PR) proteins. Another analysis, which considered various omics data, revealed that symptomatic seedlings seemed to be shifting their attention toward energy generation and storage, possibly as part of a defence strategy. They were also exhibiting stress-related signals and reactions at the same time (Jeffery Daim et al. 2023). Earlier research demonstrated that, when infected with *Beauveria bassiana* and *Lecanicillium psalliotae*, date palms exhibit notable proteomic changes. These changes are particularly evident in processes related to photosynthesis, energy metabolism, and proteins involved in cell division within in vitro-grown palms (El Rabey et al. 2016). When the date palm tree was infected with *Fusarium*

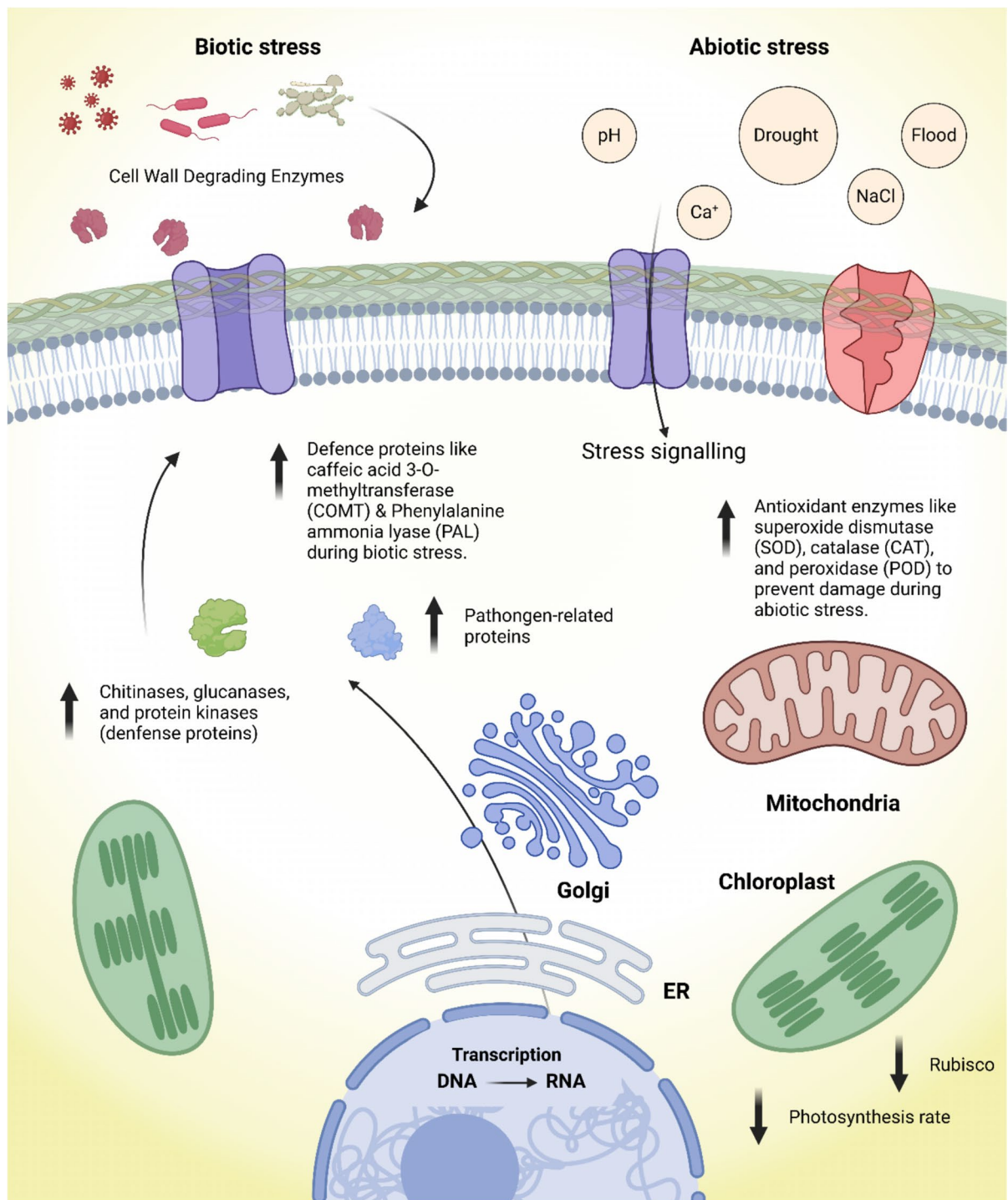


Fig. 2 A conceptual illustration showing the integrative biotic and abiotic stress response in species of the Arecaceae family. Arrows that point up and down consider the dynamics of up and down-regulation, respectively

oxysporum, proteome analysis revealed higher levels of proteins involved in protein synthesis and the metabolism of amino acid, as well as increased expression of numerous other proteins vital to basic cellular processes like housekeeping proteins, heat shock proteins, defence mechanisms, and chitin biosynthesis. Linking these proteins to the observed pathogenicity of fungus and invasive isolation (Dihazi et al. 2021). A highly destructive plant pathogen called *Phytophthora palmivora* damages economically significant tropical crops like coconut. P-loop, NTPase, and mitogen-activated protein kinase are just a few of the proteins that have been discovered by researchers studying the mycelial proteome of *P. palmivora* (Nekrakalaya et al. 2022). Large-scale proteomic research provides valuable perceptions that enhance our understanding of pathogen biology, assist in accurate genome annotation, and explain key aspects of the pathogen's vegetative growth.

Examples include the proteins linked to lignin biosynthesis from oil palm response to *G. boninense*, where this group of proteins might be useful in strengthening cell walls against fungal penetration, a trait that could potentially be targeted to high-value cultivars through selective breeding. Moreover, anti-oxidant and antimicrobial activities shown by bioactive peptides from coconut and oil palm proteins can justify their use to enhance the protection mechanisms of these plants or to promote farming applications in the form of crop-based bioproducts as well.

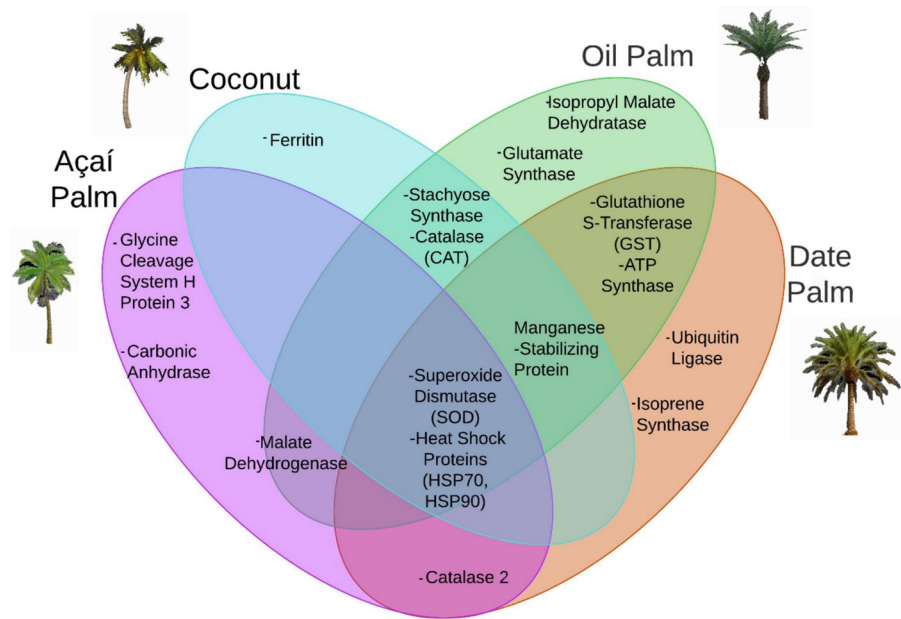
In addition, the application of proteomic data on sequence-specific nuclease genome editing such as CRISPR can allow for pinpointed modification to increase chitinases and glucanases in palms specifically designed against pathogens. The information provided by these targeted applications reveals the capacity of proteomics to provide direct insight into crop improvement strategies in palms.

Other biotic stress

Early detection is crucial because the RPW (*Rhynchophorus ferrugineus*), which frequently hides within palm trees, poses a severe threat to them everywhere. Date palm proteome expressions in weevil-infested and control palms were compared using 2D-DIGE and MALDI-TOF, with weevil-infested palms displaying notable alterations (Rasool et al. 2015). These proteins are associated with critical functions in date

palms, such as photosynthesis, carbohydrate uptake, defence responses, stress tolerance, and protein degradation. Because of their modifications under stress, they hold potential as early biomarkers for detecting red palm weevil infestations in date palms. Early detection and intervention are vital to preventing the spread of this damaging pest and ensuring effective protection for the trees (Rasool et al. 2018). A proteomic analysis of oil palm trees under various conditions, such as control, wounding, and artificial red palm weevil (RPW) larval infestation, suggests that abscisic acid (ABA) hormone signalling plays a significant role in the response to insect herbivory. Potential biomarkers for early infestation detection can help develop new detection techniques and better crop management while improving our understanding of oil palm's stress response mechanisms (Harith-Fadzilah et al. 2021). Despite the significant insights obtained from proteomic research, the full potential of proteomic platforms in biotic stress research remains largely unexplored. These platforms offer a unique opportunity to unveil previously unknown complexities, positioning proteomics as a powerful tool to deepen our understanding of the intricate nuances underlying plant defence mechanisms. Imagine the emergence of cutting-edge early detection techniques that are specifically created to identify the earliest indications of biotic stress, as well as the evolution of crop management practices into a precise science informed by proteomic insights. It goes beyond simple scientific investigation; it is a piece of innovation that blends with the complex rhythms of nature, ensuring the continued existence of the Arecaceae despite the numerous difficulties brought on by biotic stresses (Agregán et al. 2022; Gupta et al. 2023). Figure 3 highlights both shared and unique protein biomarkers across the four studied palm species, reflecting distinct and conserved biochemical adaptations to biotic and abiotic stressors. Shared biomarkers, such as SOD and Heat Shock Proteins (HSP70, HSP90), are commonly expressed across all species, underscoring their fundamental role in oxidative and thermal stress responses. Certain proteins, like Ubiquitin Ligase and Isoprene Synthase in Date Palm, and Glycine Cleavage System H Protein 3 in Açai Palm, are unique, potentially contributing to species-specific responses. Incorporating markers related to drought, cold, biotic, and abiotic stress in this analysis demonstrates the diversity of stress responses within the

Fig. 3 Venn diagram illustrating shared and unique protein biomarkers across four palm species (*Elaeis guineensis*—Oil Palm, *Phoenix dactylifera*—Date Palm, *Cocos nucifera*—Coconut, and *Euterpe oleracea*—Açaí Palm) in response to various biotic and abiotic stresses



Arecaceae family and highlights potential targets for breeding resilient palm cultivars.

A summary of research encompassing both biotic and abiotic stress, including those focused on proteomic analysis, is presented in the supplementary materials.

Flower/pollen proteomic research in the Arecaceae family

Proteomic approaches have opened up exciting new directions in understanding the intricate biology of plant reproduction and floral development. Flowers, a central factor in angiosperm reproductive success, have evolved extensively in morphology, colour, and fragrance to attract pollinators and, at times, even humans. As researchers delve deeper into these diverse floral traits, they are identifying protein candidates that may be fundamental to these unique characteristics. Integrating genomics, transcriptomics, and proteomics is now feasible thanks to recent advancements in sequencing technology (Fig. 4) (Chaturvedi et al. 2016). A comprehensive understanding of the intricate molecular networks controlling flower biology is provided by this integration. Pollen, an essential component of plant reproduction in angiosperms, has also been the focus of multidisciplinary

analyses, including transcriptomics, proteomics, and metabolomics. Understanding specific date palm pollen sensitization and the true prevalence of sensitization to this particular species depends on identifying these specific allergens in *P. dactylifera* (Postigo et al. 2009).

To assess its in vitro allergenicity, this allergen underwent purification and partial sequencing. Other IgE-sensitive spots were discovered as a result, and these had a lot in common with known allergenic proteins like 11S globulin, enolase, and isoflavone reductase (Saha et al. 2015). Furthermore, it has been determined that the allergenic properties of pollen grains from *Phoenix sylvestris* are relevant to proteomic research on pollen investigation beyond coconut pollen. In hypersensitive people, these grains are now more frequently linked to severe allergic diseases. Allergenic proteins were detected through proteomic research, six of which showed homology to known allergens while the other four were brand-new findings. Interesting cross-reactivity was observed between some of these allergens and those found in coconut pollen, including beta-conglycinin and S-adenosyl methionine synthase. One allergen in particular had a glycan moiety-based IgE binding epitope (Saha and Bhattacharya 2017).

The coconut's endosperm primarily stores carbohydrates in the early stages of development, while fatty

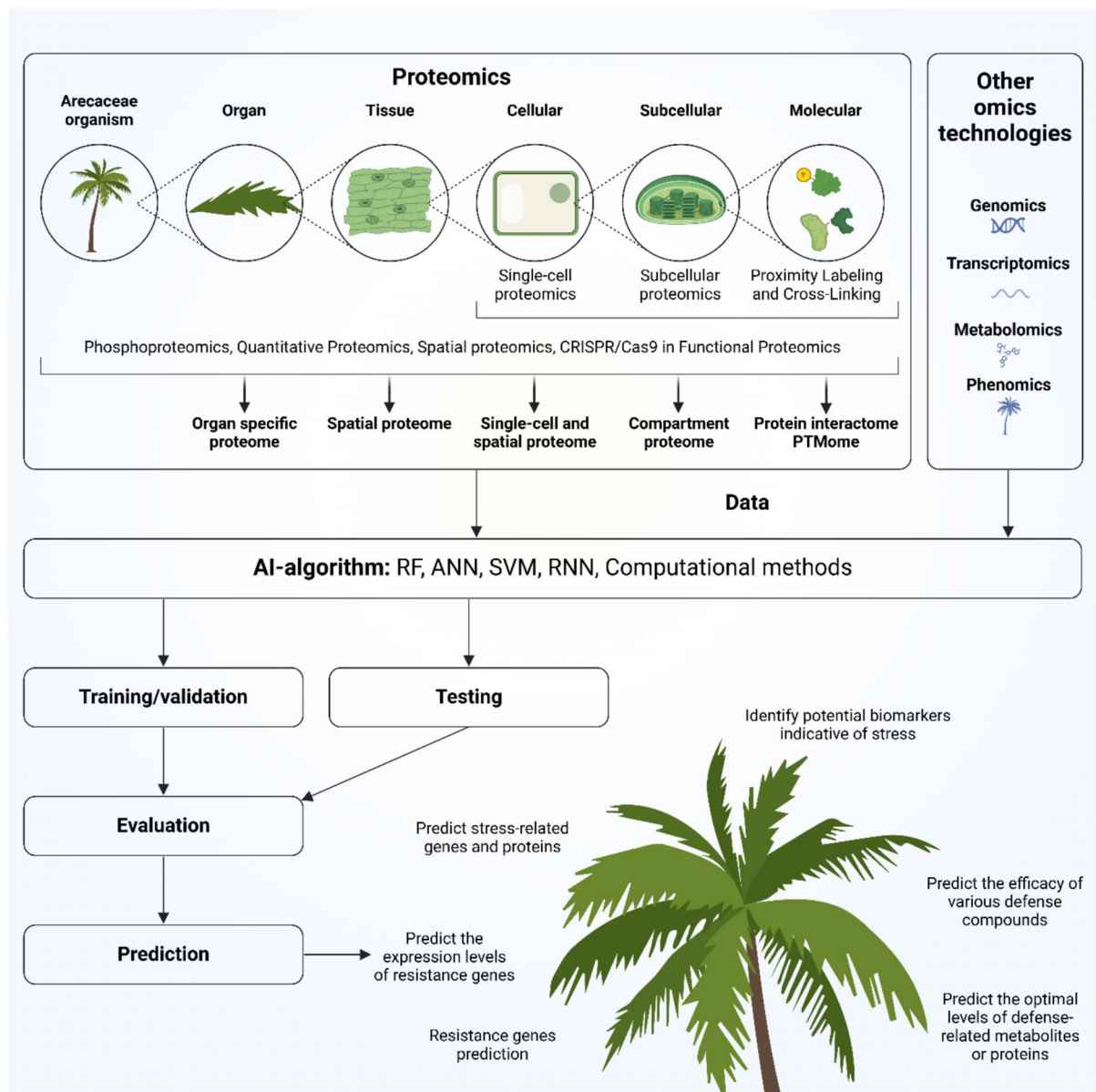


Fig. 4 An overview of proteome alterations and integrated omics techniques within the *Arecaceae* family as illustrated with omics-based approaches

acids are primarily built up in the later stages. Proteins involved in important metabolic processes, such as glycolysis, photosynthesis, and gluconeogenesis, as well as those involved in fatty acid biosynthesis and elongation, were found in coconut cultivars after proteomic analysis. Notably, the solid endosperm showed increased

accumulation of these proteins (Juarez-Escobar et al. 2021). These results highlight the distinct metabolic differences in carbohydrate and fatty acid storage across coconut cultivars, such as dwarf and tall cultivars, as well as among the developmental stages of the solid endosperm (Félix et al. 2023).

Findings across different parts of Arecaceae family members

Fruits

Coconut proteins have been shown to have a variety of potential health benefits, including antioxidant, anti-inflammatory, and antimicrobial effects. By developing a comprehensive proteomic map of the coconut genome and identifying the specific roles of coconut proteins in plant growth and development, researchers can lay the foundation for the development of new and innovative products and applications. A proteomic analysis of coconut meat has identified 1686 proteins, including antioxidants and globulins. This research aimed to provide a proteomic map of coconut proteins and identify the potential use of coconut proteins in healthcare and food stabilization (Ma et al. 2022). Earlier attempts were performed to study the protein profile of coconut samples from different sources and categorise the proteins into seven taxa (Huang et al. 2016). For oil palm research, A proteomic study investigated the proteome changes in oil palm mesocarps during maturation, shedding light on the metabolic processes and factors affecting oil yield in oil palm fruits (Loei et al. 2013). To identify the changes in protein levels during oil palm fruit maturation and factors affecting oil production in oil palm fruits, they examined the proteomic profiles of mesocarps at four developing stages—12, 16, 18, and 22 weeks after pollination—by 8-plex iTRAQ labelling coupled to 2D-LC and MALDI-TOF/TOF MS. Proteins from some essential metabolic pathways, such as glycolysis, fatty acid biosynthesis, pentose phosphate shunt, starch and sucrose metabolism, and oxidative phosphorylation, were discovered to be variably expressed in a coordinated way.

A comparative proteomic approach was employed to study proteome changes during early fruit development stages. This study employed a 2-DE gel-based proteomic comparative analysis on developing oil palm fruits to identify specific protein species and changes in abundance during early fruit development. Remarkable changes in protein abundance were observed throughout the development (Kok et al. 2021). Protein biomarkers have been conducted for identifying the maturity stage of the oil palm somatic embryo including the expression of sister chromatid cohesion PDS5 and E3 ubiquitin-protein ligase,

which are only expressed in the somatic embryo and plantlet (Aroonluk et al. 2019).

A proteomic analysis employing two-dimensional electrophoresis to characterize the proteins in date palm sap. The proteins were found in the juice extracted from the Deglet Nour cultivar of date palms (*Phoenix dactylifera* L.). 52 of the more than 100 spots visible in the SDS-PAGE patterns were recognized. *Saccharomyces cerevisiae*, which may be a naturally occurring microflora in date palm sap, was linked to a few of these proteins. These results therefore indicated that xylem sap has a panel of antioxidants, protein, growth-promoting, and antifungal capabilities (Thabet et al. 2010).

Protein abundance varied between embryonic stages, which was found to be correlated with metabolic requirements of the pericarp tissues of the açai fruit. The investigation also disclosed the existence of secondary metabolites in açai which had not been previously reported (Andrade et al. 2020).

De Oliveira et al. (2019) investigated how young açai plants react to drought using proteome profiling. Stress proteins and metabolite production are caused by signal pathways that are activated by the depletion of soil and water. Essential protein synthesis shields against photodamage in low light. During drought, alterations in carbonic anhydrase were identified by the proteomic profile. Carbonic anhydrase (chloroplastic isoform X2) levels in stressed plants did not change after a moderate drought, but they did dramatically decline during a severe drought. To learn more about how the species responds to drought, more research is required to examine proteins connected to the process of photosynthesis transpiration, and the antioxidant system (de Oliveira et al. 2019).

Four stages of growth were examined in the analysis of açai palm seeds, which are abundant in mannan for D-mannose or ethanol and health-promoting polyphenols. Out of 2465 proteins, 524 showed unique abundance profiles. From stages S1 to S3, there was a noticeable rise in enzymes associated with nucleotide-sugar biosynthesis, specifically GDP-mannose generation, which indicated dynamic alterations in proteomics (Neto et al. 2023).

Using 2-DE map analysis, significant differences were found in the protein extracts of date palm somatic and zygotic embryos, with both qualitative and quantitative differences found in 60% of consistent sites. Variable spots were also discovered by

MALDI-TOF-TOF MS analysis, which shed light on the molecular differences between the date palm somatic and zygotic embryo proteome profiles (Sghaier-Hammami et al. 2009). In oil palm fruits, the mesocarp and exocarp show high protein abundance related to fatty acid and secondary metabolism, while kernel and shell proteins focus on storage functions. Key enzymes linked to stilbenoid biosynthesis—4CL, HCT, and ROMT—are expressed mainly in the exocarp, mesocarp, and shell, supporting distinct metabolite profiles across tissues. These findings offer insight into the tissue-specific metabolic roles essential for optimizing oil palm resource use (Has-san et al. 2024).

Leaves

Proteomic methods were used to examine mature oil palm leaves, and 191 protein spots were identified, with 35 satisfactorily described, suggesting roles in photosynthesis, cellular biogenesis, metabolism, response to stress, and transport (Tan et al. 2017). An earlier study examined leaves from palm trees with varying growth rates, identifying 40 differentially abundant protein spots using real-time PCR and highlighting potential biomarkers such as L-ascorbate peroxidase, triosephosphate isomerase, and superoxide dismutase, providing insights into oil palm growth and development (Tan et al. 2016).

Using comparative 2DE and LC-QTOF MS/MS to investigate *G. boninense* infection in oil palm, Daim, Ooi, Ithnin, et al. (2015) discovered 51 proteins related to photosynthesis and the breakdown of glucose in addition to 54 altered protein positions. This highlights how fungal pathogen infection affects oil palm leaves, changing the expression of proteins involved in immunity, defence, transpiration, and glucose metabolism (Jeffery Daim et al. 2015). Proteomic study of oil palm leaves inoculated with *Ganoderma* spp. showed 82 resolved proteins, 24 of which were shown to be differently expressed in response to infectious *G. boninense* and *Ganoderma tornatum*. These proteins, which have roles in signalling, stress/defence, photosynthesis and regulation of energy, may have a role in disease susceptibility. Both *Ganoderma* species caused changes in abundance, demonstrating their influence on their relationship with oil palm leaves (Al-Obaidi et al. 2016a).

The study of *Elaeis oleifera* x *Elaeis guineensis* crosses for somatic embryogenesis stimulation focused on finding proteins associated with different responses. The responsive genotype displayed stress management at 90 days throughout a 180-day induction phase, allowing energy use for cellular growth by 150 days. This highlights the significance of proteins associated with oxidative damage, protein manufacturing, metabolism of energy, and growth (Almeida et al. 2019).

Research on date palm leaves' proteomes has provided information on diseases of plants and stress reactions. To identify qualitative and quantitative changes in protein accumulation between infected and control palms, Gómez-Vidal and his group analyzed entomopathogenic fungi using 2-DE analysis and MALDI/TOF-TOF. The study emphasized elevated proteins associated with defence or stress response in plants when entomopathogenic fungi colonize them (Gómez-Vidal et al. 2009). In a different research, Marqués and colleagues used 2D-DIGE to find differences in the amount of protein in damaged as well as unaffected date palms. Stress response was suggested by increased amounts of other proteins in the afflicted tissue. The significance of proteome research in understanding the molecular mechanisms behind plant illnesses and stress reactions is highlighted by these results (Marques et al. 2011). Date palm (*Phoenix dactylifera*) adjusts its photosynthesis-related proteins, stress-related proteins, and secondary metabolic processes despite adverse environments. A substantial protein response including heat shock proteins and antioxidants is reported under severe circumstances. Particularly, the discovery and characterisation of individual genes, such as isoprene synthase, provide light on molecular adaptation (Ghirardo et al. 2021). This protein plasticity promotes plant tolerance to environmental challenges, demonstrating their adaptability to changing environments. The red palm weevil (*R. ferrugineus*) is a severe hazard to palm trees globally. The proteome of infected date palm leaves was investigated using 2D-DIGE and MALDI-TOF. There were qualitative and quantitative differences in proteomes. The study revealed proteins involved in plant stress, defence, photosynthesis, carbohydrate intake, and protein breakdown. These proteins have the potential to be early red palm weevil indicators in date palm trees, underscoring the importance of the findings for pest control (Rasool et al. 2018). The

reactions of two coconut cultivars to cold stress were investigated using iTRAQ-based proteome profiling. Proteins identified were linked to secondary metabolite production, respiration, photosynthesis, and stress responses. When compared to the fragrant coconut type, the cold-tolerant Hainan Tall variant has a higher quantity of stress-responsive proteins. Photo-damage may be reduced if the quantity of photosynthesis-related proteins is reduced in response to cold stress, assisting in low-temperature adaptation (Yang et al. 2020).

Roots

Basal stem rot caused by *Ganoderma* spp. is a global hazard to oil palm productivity. Changes in enzyme activity reflect the oil palm's efforts to strengthen its defences. On the other hand, *Ganoderma* mycelium proteomic has also been investigated to determine the pathogenicity of these species in comparison to other less invasive species (Zakaria 2022). Both *Ganoderma* spp. increased the expression of basic leucine-zipper (bZIP) transcription factors, implying a role in fungal attachment and colonization of oil palm roots. Proteins like triose-phosphate-isomerase have been linked to surface adherence, which could help with fungal attachment and invasion. During the mycelium-root interaction, redox signalling proteins, specifically redoxin/peroxiredoxin, were highly expressed, highlighting the role they play in early *Ganoderma* pathogenicity in oil palm. *G. boninense* pathogenicity and root tissue penetration may be aided by alpha-amino adipate reductase, which is known for its role in lysine biosynthesis (Dzulkaifi et al. 2023; Al-Obaidi et al. 2017).

Bioactive peptides in the Arecaceae family

The Arecaceae family is rich in bioactive compounds, mainly lipophilic, such as polyunsaturated fatty acids, carotenoids, and vitamin A. Their fruits have been reported to have the potential to be used to prevent non-communicable diseases, such as diabetes or obesity, and to promote health (de Souza et al. 2020). More recently, bioactive peptides, which are encoded by primary proteins and have bioactivity when released from the original protein, have been studied. Therefore, they can be released during in vivo digestion or during processing, such as enzymatic

hydrolysis in vitro (Singh et al. 2023). However, investigations on bioactive peptides and their health effects are scarce (Morais et al. 2022).

In the Arecaceae family, the richness of bioactive peptides has been little explored, especially through proteomic approaches, which has limited the discovery of bioactive peptides in coconut and palm trees, as well as their by-products. This by-products-based approach would allow commercially valuable bioactive peptides to be obtained from plant by-products (Görgüç et al. 2020). Many agro-industrial products, such as coconut pulp, contain large percentages of proteins (10–50%) and could be sustainable sources of bioactive peptides (Berenguer et al. 2023). For instance, when the proteome of coconut meat was investigated using a shotgun approach, antioxidant proteins, globulins, and their corresponding bioactive peptides with potential applications as antioxidants and emulsifiers were identified (Janssen et al. 2022). Other authors have studied bioactive peptides from *Cocos nucifera* L. and their encapsulation in maltodextrin-pectin and maltodextrin to mask their bitterness (Sarabandi et al. 2024). Dates could also have potential health-promoting benefits due to their bioactive compounds, including the agricultural by-products of date trees (Maqsood et al. 2020). Peptides with crop protection and health activities were found in the mesocarp of oil palm fruit. Enzymatic hydrolysis-derived peptides from the mesocarp inhibited the growth of *G. boninense*, and had antimicrobial properties found by in silico approaches (Chung et al. 2022). On the other hand, bioactive peptides derived from palm kernel cake protein hydrolysates showed angiotensin-I converting enzyme (ACE) inhibitory activity through in vitro and in vivo assays, whose sequences are YGIKVGYAIP, YLLLK and LPWR-PATNVF (Zarei et al. 2022). Other bioactive peptides were also isolated from glutelin-2 hydrolysates from palm kernel expellers, and their antihypertensive properties were studied against ACE, both in vitro and in vivo. Four new peptides with Leu-Pro-Ile-Leu-Arg, Val-Ile-Glu-Pro-Arg, Val-Val-Leu-Tyr-Lys, and Ala-Asp-Val-Phe-Asn-Pro-Arg sequences were identified (Zheng et al. 2017). In another recent study, two bioactive peptides from *Phoenix dactylifera*, U3 and U7, were found to be successful in the treatment of breast (MCF-7 and T47D) and liver (HepG2) cancer and had a synergistic effect with mitonane (Baothman et al. 2024).

Macauba (*Acrocomia aculeata* L.) kernel proteins, primarily consisting of 11S and 7S globulins, demonstrate high nutritional potential due to their richness in essential amino acids, particularly methionine and cysteine. This composition, combined with unique solubility properties under varying pH and ionic conditions, positions Macauba proteins as a valuable plant-based protein source with applications in food supplementation, especially as a complement to legume diets (Toledo e Silva et al. 2021).

In this context, the plant peptidome is a growing field (Smolikova et al. 2020), and should receive more attention in the Arecaceae family. Further research on the identification and elucidation of the mechanisms of action of peptides of the Arecaceae family through in vitro, in vivo, and in silico assays is desirable to find therapeutic applications in diseases such as cancer, diabetes, and cardiovascular disorders (Al-Karmadi and Okoh 2024). As a result, these bioactive peptides could potentially be used in food, pharmaceutical and cosmetic formulations to improve public health (Ye et al. 2022).

Challenges and limitations of Arecaceae family proteomics

Proteomics of non-model organisms presents challenges and limitations in terms of both techniques and data interpretation. The *Arecaceae* family is distributed in five subfamilies, with 181 genera and 2600 species, and a large intraspecific diversity (de Melo et al. 2024). Each cultivar and variety is characterized by size, shape, colour, texture, and flavour (Al-Karmadi and Okoh 2024).

Consequently, several proteomic approaches have been developed in the last decade and applied in the study of the *Arecaceae* family, ranging from gel-based to gel-free strategies, and recently, targeted approaches.

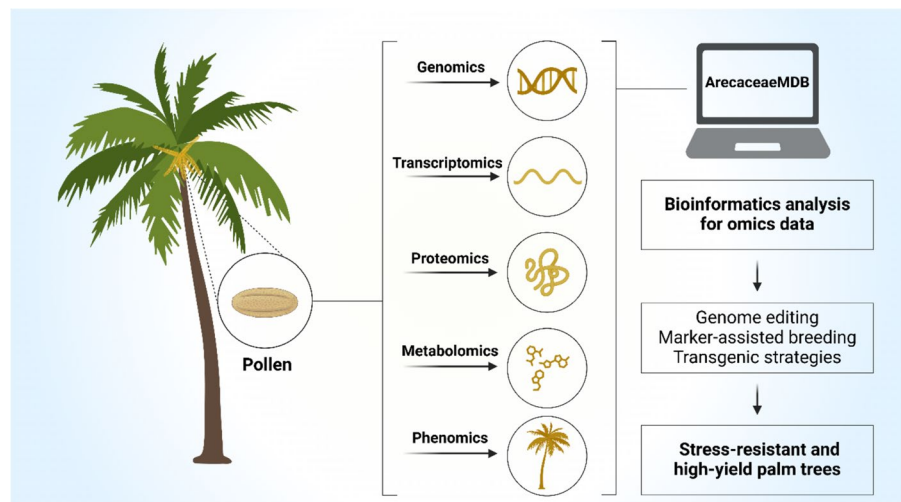
Protein identification relies on well-annotated genomes, protein databases, mass spectra, RNA, and DNA (Jorrin Novo 2021). However, a challenge in the proteomics of the *Arecaceae* family is that many species lack complete genomic, transcriptomic, and proteomic resources. Even though the members of this family are of great ecological and economic importance. Plants like date palms, present challenges due to their dioecious nature, requiring specialized genome assembly software, as well

as additional considerations (Ramesh et al. 2024). Current genomic assemblies correspond to those of economically important species, such as *Elaeis guineensis* Jacq, *Phoenix dactylifera* L, *Cocos nucifera* L, *Areca catechu* L, *Calamus simplicifolius*, and *Daemonorops jenkinsiana*. These genomic assemblies were complemented by resequencing and transcriptomics, leading to further multi-omic research. As a result, the Arecaceae Multi-omics database ArecaceaeMDB (<http://arecaceae-gdb.com>) hosts the genomes of six economically important palms. This database may also overcome challenges in understanding protein–protein interaction networks in Arecaceae species. For instance, previous reports have analyzed protein–protein interactions using STRING software (v. 11.0, <https://string-db.org>), although different reference organisms were used. Oil palm proteins were blasted against *Musa acuminata* (Al-Obaidi et al. 2016b) and coconut meat proteome proteins of *C. nucifera* against *P. dactylifera* L. (Ma et al. 2022).

The ArecaceaeMDB database represents a significant advancement in the field, enabling researchers to conduct integrated multi-omics analyses for Arecaceae species (Fig. 5). By offering consolidated genomic, transcriptomic, proteomic, and metabolomic data, the platform allows for the exploration of stress-responsive pathways and the identification of potential markers for breeding programs (Yang et al. 2023). This database supports efforts to enhance stress tolerance in Arecaceae species by enabling detailed cross-species comparisons and the identification of conserved pathways that contribute to resilience against environmental stressors.

For the next decade, the main challenges can be set at experimental, analytical, dry, and wet levels. Future approaches may also be based on the proteomics study of a cell type, as single cells may be almost impossible with the available technology. There is also a challenge in databases that must integrate proteomic data to create interconnected repositories. In this regard, ArecaceaeMDB will continue to add more published omics data, and new data analysis tools to benefit genetic and functional research, as well as to promote industrial applications of the Arecaceae family. Finally, the challenge of developing new and cheaper methods must be overcome by developing less expensive techniques that are applicable in various sectors.

Fig. 5 Integrative multi-omics approach for enhancing palm tree resilience and productivity. Pollen from palm trees is analyzed through genomics, transcriptomics, proteomics, metabolomics, and phenomics to gather comprehensive biological data



Summary of key findings and further research

Proteomic techniques have had a transformational impact on palm research, demonstrating extraordinary adaptability across five critical areas. First, proteomic research revealed detailed biological functions by identifying important proteins required for photosynthesis, stress responses, defence systems, and plant metabolism. Second, proteomic research increases disease understanding and management by finding disease-associated proteins, unravelling processes, and discovering possible biomarkers for early detection and focused management. Furthermore, these methodologies enable comparative analysis across several palm species, providing useful insights into genetic variants, stress tolerance, and protein expression differences. Beyond just identifying proteins, proteomics allows researchers to dive into the complex constitution of plants, improving our understanding of development, growth, and stress management which directly supports the identification of candidate proteins and pathways relevant for molecular breeding and genetic improvement programs. Such insights are vital for selecting stress-resilient cultivars and improving yield traits, paving the way for practical applications in palm breeding, precision agriculture, and sustainable crop production.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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