



TRANSCRIPTOME ANALYSIS REVEALS THE GROWTH-DEFENSE TRADE-OFF IN *ACACIA MANGIUM* UPON *CERATOCYSTIS* INFECTION

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INTRODUCTION

Plants and pathogens communicate with one another within their environment. This communication is called plant-pathogen interaction. During compatible interaction, the pathogen manipulates the immune system of the host plant which leads to susceptibility. On the other hand, while in incompatible interaction, the plant prevents invasion of the pathogen by inducing various defense mechanisms such as increase lignin production, synthesis of phytoalexins, hypersensitive reaction and production of secondary metabolites. In order to understand the plant-pathogen interaction comprehensively, it is crucial to monitor the gene expression profiles of both interacting organisms simultaneously in the same infected plant tissue.

In recent years, *Ceratocystis* wilt disease has emerged as a devastating threat to *Acacia mangium* plantations in Malaysia, particularly in Sabah, Sarawak, Pahang and Johor. The fungus, *Ceratocystis fimbriata* attacks *Acacia* trees by entering through small openings or wounds caused by unsound silviculture practices as well as wounds caused by animals like elephant and wood-boring insects (Mohd Farid et al. 2017). *C. fimbriata* would slowly kill the host cells and tissue to derive nutrition from dead cells, proliferate within the vascular tissue, disrupt water translocation and cause typical wilt symptoms (Van Wyk et al. 2007). Additionally, studies by Mohd Farid et al. (2017) have reported that *C. fimbriata* killed *Acacia* seedlings within five weeks after inoculation process.

Presently, the molecular mechanisms regulating defense response of *A. mangium* towards *Ceratocystis* are yet to be fully understood. There has been an emerging new technology, called next-generation sequencing (NGS). Transcriptome sequencing via NGS technology has been successfully carried out to

investigate plant-pathogen interaction between palm oil and *Ganoderma boninense*, banana and *Fusarium oxysporum*, rice and *Magnaporthe oryzae* as well as black pepper and *Phytophthora capsici*. This high-throughput technology plays a vital role in elucidating the mechanisms behind altered gene expression as compared to the conventional approaches like microarray and northern blot.

Concept of growth-defense trade-off in plant

Upon infection by pathogens, plants will activate a complex series of responses in order to defend themselves. One of the responses is growth-defense response. According to Huot et al. 2014, the activation of defense generally occurs at the expense of plant growth which is known as 'growth-defense trade-off'. Smakowska et al. (2016) demonstrated that this trade-off occurs in plants due to resource limitations, which demand prioritization either to grow or defend, depending on external and internal factors. Furthermore, studies indicated that growth inhibition due to activation of defense responses is not a default program. This antagonistic relation between growth and defense happens as a result of incompatible molecular pathways or sharing of signaling components between the programs (Eichmann and Schäfer, 2015). Understanding the molecular mechanisms used by plants to balance growth and defense is crucial because it can enrich plant breeding and genetic engineering strategies for selection of elite genes that will increase plant fitness. This article discusses the evidence supporting the concept of growth-defense trade-off in *A. mangium* upon *Ceratocystis* infection as well as the recent advances in elucidating the molecular mechanisms underlying its occurrence.

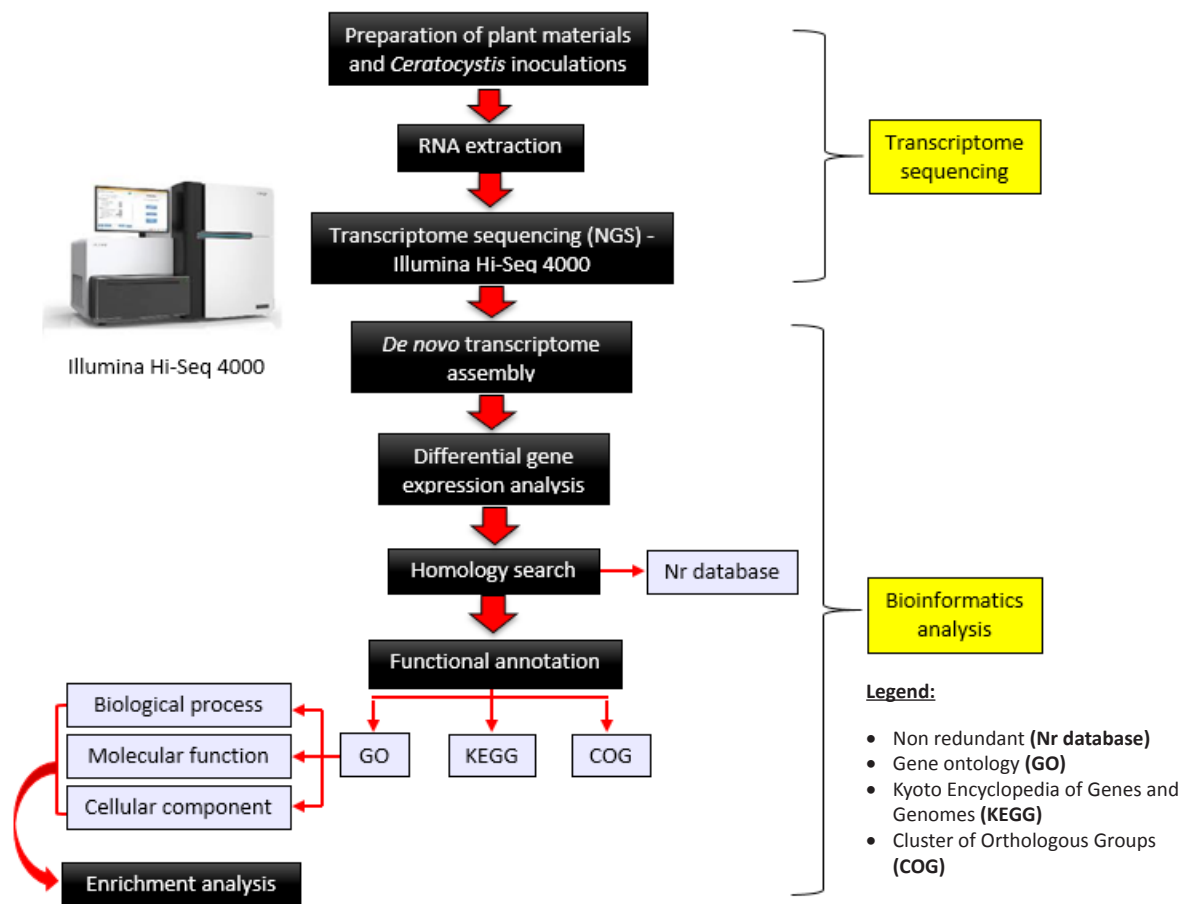


Figure 1 Workflow of transcriptome sequencing and bioinformatics analysis performed to reveal the growth-defense trade-off concept in *A. mangium* infected by *Ceratocystis*

Transcriptome analysis is performed to reveal the growth-defense trade-off concept in *A. mangium* infected by *Ceratocystis*

Transcriptomics is the technique to profile all the transcriptional changes that occur in cells or tissues of plants and pathogens during plant-pathogen interaction. Presently, transcriptomics is in its golden era and researchers around the globe are successfully applying it to reveal underlying mysteries of the plant-pathogen interaction (Chakraborty & Basak, 2017). In the current study, transcriptome sequencing was performed on infected and non-infected *A. mangium* to understand molecular pathways regulating plant growth and defense towards *Ceratocystis* infection. Figure 1 showed the detailed workflow involved in this study.

Up-regulation of defense genes and down-regulation of growth-signalling genes in molecular pathways upon *Ceratocystis* infection

The Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway analysis revealed that most of the up-regulated genes were involved in protective activities

pathways like phenylpropanoid pathway, biosynthesis of antibiotics and flavonoid pathways. Antibiotics are phytochemicals that are known to have antimicrobial and antiviral properties in plants (Wink & Schimmer, 2010). Considering the aforementioned properties, the activation of genes in this pathway might be one of the main defense mechanisms in *A. mangium* against *Ceratocystis* infection. Phenylpropanoids exhibit antimicrobial activity which plays major role as chemical and physical barriers against pathogen infection. They also act as signal molecules in local and systemic plant defense mechanism. The phenylpropanoid pathway is linked to flavonoid biosynthetic pathway which also plays important role in plant resistance (Treutter, 2006). The overproduction of phenylpropanoids and flavonoids by the plant is considered to be a part of a specific antimicrobial defense system (Wink & Schimmer, 2010). Therefore, the activation of genes like peroxidase (POD, EC:1.11.1.7), cinnamyl-alcohol dehydrogenase (CAD, EC:1.1.1.195) and O-hydroxycinnamoyl transferase (HCT, EC:2.3.1.133) in phenylpropanoid pathway and chalcone isomerase (EC:5.5.1.6), flavanone (EC:2.3.1.74) and 4-reductase (EC:1.1.1.219) in flavonoid pathway reconfirmed their important involvements in plant defense response.

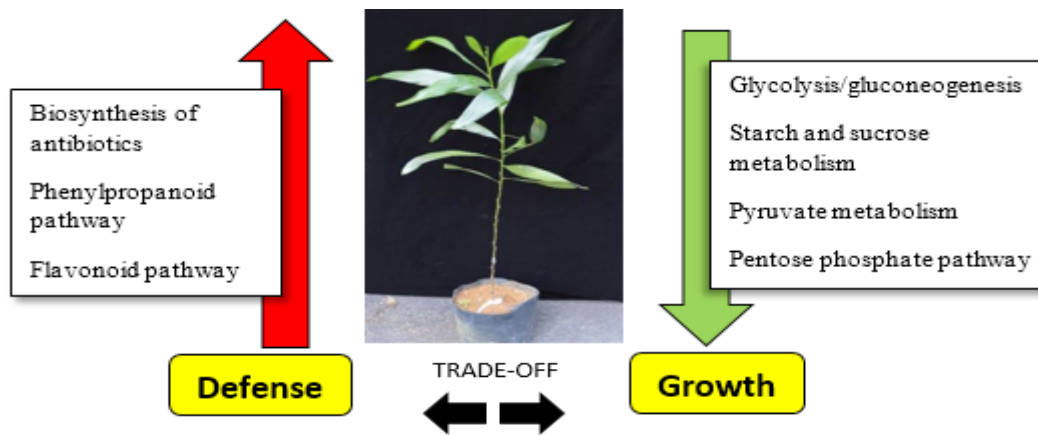


Figure 2 Illustration of the concept of growth-defense trade-off in *Acacia mangium* upon *Ceratocystis* infection

Figure 2 illustrated that genes associated with defense response were highly up-regulated while genes related to growth and development processes were down-regulated upon *Ceratocystis* infection. Glycolysis/gluconeogenesis, starch and sucrose metabolism, pyruvate metabolism and pentose phosphate pathway have important functions in plant growth and development. This finding supported the hypothesis that there was a trade-off between growth and defense response. The activation of defense genes like POD, CAD, HCT and chalcone isomerase genes will suppress growth and tighten up the cell walls so that the cells can build more solid barrier to prevent penetration of *Ceratocystis*, thus increasing disease resistance in *A. mangium*. The results showed that the growth-defense trade-off was caused by the incompatibility of the molecular pathways regulating plant growth and defense.

Benefits and future perspectives

Advances in NGS technology have created powerful techniques in elucidating molecular mechanisms underlying plant-pathogen interaction. Comprehensive understanding on the specific molecular interactions regulating the growth-defense trade-off will provide a foundation to formulate breeding strategies in producing clones or varieties to adapt to the fluctuating environmental conditions. Furthermore, it is important to untangle this antagonistic relation as both growth and defense are vital for plant survival, reproduction and fitness. Lastly, this knowledge will be useful for the researchers to improve plant biomass without impairing plants' ability to defend themselves against pathogens.

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Plant growth and defence are two important processes vital to the survival and adaptation of a plant to its surroundings. Previously, growth-defense trade-off in plants was thought to occur due to resource or energy limitation. This article addresses the misconception of the theory and specifically clarifies the actual underlying reasons of this occurrence in *Acacia mangium* upon *Ceratocystis* infection through technology advances, known as next-generation sequencing (NGS). Understanding the molecular basis behind this trade-off in plants is important to improve plant breeding strategies in order to produce high-quality planting materials to adapt to diverse environmental challenges.

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