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Editorial

Growth–Immunity Tradeoff in *Brassica* Crops

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1. Introduction

In recent decades, the research community evidenced that plants affected by pathogens and pests may display delayed development. This phenomenon can be partially explained by the destruction of photosynthetic tissues, but this is not the only cause. Any defense response, i.e., the production of induced chemical defenses, is costly in terms of plant resources and energy investment, and a tradeoff may exist with other plant functions, such as growth or reproduction, which could negatively impact plant fitness and biomass production [1–5]. This activation of defense mechanisms at the expense of growth inhibition is known as the "growth-immunity tradeoff" phenomenon. This is an adaptive strategy to protect against pathogens and pests when necessary while conserving energy for growth in less challenging conditions [3]. For a long time, it was thought that the "dilemma of plants to grow or defend" was a simply model, where elevated defense is based on a shift from metabolic resources to defense [6]. However, the costs derived from defenses are evident even in environments where nutrients are unlimited and, theoretically, the plant could grow and defend itself optimally [7]. This fact highlights that behind this phenomenon, a complex and precise coordination of plant growth and metabolism through immune signaling pathways may be in place. Multiple cellular mechanisms are in charge of this imaginary balance, involving gene transcription, molecular signaling and metabolism [8–10].

Pest and pathogens cause significant yield and economic losses in agricultural systems. Therefore, increasing resistance to biotic stresses is a desired strategy in crop breeding. However, the costs associated with enhanced resistance may also have an impact on crop production. Therefore, knowledge of how this balance is produced and regulated is of vital importance when deciding on the best strategy to improve crop resistance [11–13].

2. Evidence of Growth–Immunity Tradeoff in *Brassica* Crops upon Pathogens' Attack

Brassica crops have significant relevance for human nutrition, as they are important contributors to daily food supplies worldwide [14]. Several studies have provided valuable insights into the resource allocation mechanisms in *Brassica* crops, enabling them to strategically prioritize either defense or growth to optimize survival and fitness in response to the diverse demands derived from pathogens' attachment [9,15–21].

Evidence of a growth–immunity tradeoff has been documented in *Brassica napus*. Even in the absence of the pathogen, a *Peronospora-parasitica*-resistant variety of *B. napus* exhibits a developmental delay compared to susceptible varieties. This occurs due to the action of a single gene, which constitutively increases the defenses at the expense of plant growth [9]. Growth–immunity tradeoffs are regulated at a transcriptional level in the *B. napus*—*Sclerotinia sclerotiorum* pathosystem. The silencing of MYP43 in *B. napus* decreases growth and increases resistance to *S. sclerotiorum* [19]. The transcription of WRKY33 is activated in *B. napus* by an MAPK cascade after infection by *S. sclerotiorum*, enhancing phytoalexins' accumulation early in the infection. During late-stage infection, the WRKY28 transcription is induced, suppressing the transcription of WRKY33 and activating growth factors [17].

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Defensive hormones play a crucial regulatory role in balancing growth and immunity. In the *B. napus-Leptosphaeria maculans* pathosystem, the early increase in salicylic acid was correlated with the prioritizing of defenses versus growth. However, when salicylic acid, jasmonic acid, and ethylene were activated in a balanced manner, both growth and defense mechanisms were concurrently promoted [18]. Growth hormones are also involved in the regulation of the growth–immunity tradeoffs in *Arabidopsis thaliana*. Specifically, jasmonic acid, a key regulator of basal and induced defence metabolite accumulation, such as glucosinolates, and defensive structures, is influenced by auxins, cytokinins, gibberellins and brassinosteroids [20].

Brassica oleracea is highly susceptible to black rot disease, triggered by the bacterium *Xanthomonas campestris* pv. *campestris* [22]. We found that seedlings of several crops of *Brassica oleracea* (cabbage, kale, cauliflower and broccoli) showed weight loss during black rot disease [16,21] as a possible consequence of the allocation of resources towards defense mechanisms rather than growth. This hypothesized growth–immunity tradeoff is supported by the optimal defense hypothesis, since the effect was found in seedlings, which are the most inclined to induce defenses [20]. Therefore, we decided to explore the following question: Can *X. campestris* pv. *campestris*, the causative agent of black rot disease, exert pressure on the *Brassica* crops to prioritize either growth or immunity?

3. Growth–Immunity Tradeoff in *Brassica oleracea* Infected by *Xanthomonas campestris* pv. *campestris*: A New Vision

After exploring the cited tradeoff in two *B. oleracea* lines differing in their resistance in depth, we found that the loss of plant´s biomass upon infection was related to the increment in the expression of key genes of the synthesis the ethylene hormone (resistant line) and salicylic acid hormone (susceptible line) [16]. The hormonal alterations favored the activation of defenses, such as the synthesis of glucosinolates, phenolic compounds and stomatal closure, at the expense of growth and development. After analyzing the activation of these defenses, we concluded that the loss of biomass can be partially related to a reallocation of resources through the defensive metabolism.

However, an additional mechanism could be involved in the biomass loss during infection. Surprisingly, the loss of biomass was mainly due to the accumulation of starch and the immobilization of free sugars [16]. These results expand the concept of tradeoff, emphasizing the role of primary metabolites in the defensive strategies of plants against pathogens. They are reallocated to synthetize defensive compounds but also play an active role in plant defense by restricting the contribution of nutrients to the pathogen, despite causing a slowdown in the growth of the plant itself.

4. Future Implications

The recent advances in the *B. oleracea*—*X. campestris* pv. *campestris* pathosystem expand the current information about tradeoff mechanisms. Our results suggest that the decrement in plant development is mainly due to the down-regulation of primary metabolism, and the immobilization of sugars, employed as a defense strategy. This completes the current vision of plant immunity. Any advances in this matter present exciting prospects for the future to enhance resistance and combat crop diseases.

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