Plant Growth-Defense Trade-Offs

Subjects: Agriculture, Dairy & Animal Science

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In order to survive in a hostile habitat, plants have to manage the available resources to reach a delicate balance between development and defense processes, setting up what plant scientists call a trade-off. Most of these processes are basically responses to stimuli sensed by plant cell receptors and are influenced by the environmental features, which can incredibly modify such responses and even cause changes upon both molecular and phenotypic level.

growth-defense trade-offs phytohormones

1. Introduction

Plants, as sessile organisms, are often facing various abiotic and biotic stresses that induce physiological, biochemical, and molecular changes, which are finally reflected in terms of lowest growth and productivity. Plant stress tolerance and susceptibility are governed by a complex exchange of signals and responses occurring at cellular and molecular levels. So, plant resistance relies strongly on timely stress recognition and the rapid and effective activation of defense mechanisms[1]. The response of plants is dynamic and complex and varies with the nature of these stresses, i.e., defense mechanisms for pathogen infection or drought stress conditions are different.

Plant immune responses are also modulated by abiotic signals such as light and temperature as well as the circadian clock [2]. In the absence of perceived pathogens or environmental changes, young tissues must suppress immune or adaptation responses to maximize growth, whereas mature organs can be more prepared for defense[3]. Thus, the activation of defense mechanisms at the expense of growth suspension is known as the “growth-defense trade-off” phenomenon (GDT) and is the result of a delicate balance between growth and defense or adaptation responses. Competition for limited amount of available resources has been considered as the driving force for trade-offs[4][5][6][7], but recently it has been proposed that instead this could be the result of opposite molecular pathways regulating growth and defense[8][9].

Due to climate change that is impacting negatively agricultural crops production worldwide, GDT have acquired increasing importance from the ecological, agricultural, and economic point of view. For centuries, agricultural crops have been bred with the main goal of maximizing growth and yields. As a consequence, plants have diminished its genetic diversity for abiotic stresses defense[10]. The knowledge about the molecular and regulatory aspects that manage the above-mentioned phenomenon is the very first step in the development of new agricultural products that stimulate both growth and defense responses. Thus, in this review, we intend to make an interesting approach to the GDT aimed to suggest elements for the analysis and better understanding of key pieces of knowledge involved in further development of agricultural applications.

2. GDT Influence over Secondary Metabolism

Trade-offs take part in the secondary metabolism as well, and hence depending upon the conditions and features of the environment where the plant is in, the nature and concentration of secondary metabolites change. Secondary metabolites are necessary for a ubiquitous amount of processes that involve transduction, cell adaptation and survival, communication, and protection, but the role of secondary metabolism upon defense and defense response has been comprehensively studied in the last decade[11]. Transcription factors responsible for regulating the expression of secondary metabolites biosynthesis genes, are the result at molecular level of a response that was first activated by an intra- or extracellular signal perceived by the membrane receptors, in a similar way as explained above in this review[12].

The concentration of secondary metabolites could serve as reference to know about the development stages and conditions of the ecosystem that surrounds the plant organism: instances of nutrients availability, stress condition, herbivore attack, and some others. The accumulation and cell secretion of nicotine and caffeine in tobacco and coffee plants, respectively, upon tissue wounding, that could be interpreted as herbivore attack, could explain the insecticide activity of these compounds [13][14]. The high conjugation displayed in anthocyanins' structure allow them to interact with light and absorb some kinds of radiations, thus its production is stimulated under high-light exposure. As they also are really good antioxidants, conditions such as nutrients deficiency, and pathogen attack and wounding, may induce an over production of anthocyanins[15][16]. In leaves and stem of *Tithonia diversifolia*, the production of sesquiterpenes, lactones as tagitinin A and C (tagitinin C with potent cytotoxic activity on human malignant cells[17]) and phenolics as 5-*O*-caffeoylquinic acid (Figure 1) is determined by the amount of rainfall and temperature changes occurring with seasonal variation[18]. On the other hand, the production of phenolics and subsequent incorporation in plant cell wall as suberin or lignin is increased by cold stress[12], while tree adaptation was associated with production of chlorogenic acid at high levels[13].

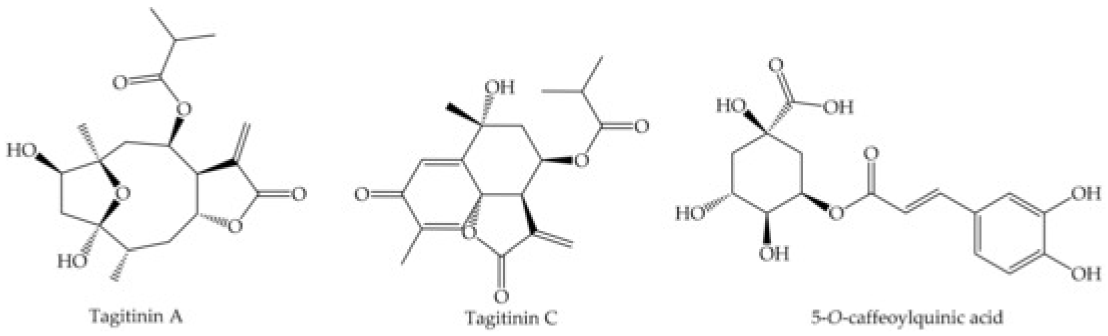

Figure 1. Chemical structures of tagitinin A, C and 5-*O*-caffeoylquinic acid detected in *T. diversifolia* extracts.

Some secondary metabolites are volatile organic compounds (VOCs), so they can spread along and establish a sort of interaction within the plant itself and with its similar ones on the field-side. Moreover, it was recently proposed that these compounds may work in synergy with other secondary metabolites and hormones which are all synthesized to regulate senescence[19]. For instance, the synergism between the production of isoprenoids and biosynthesis of cytokinins turns out in increased antioxidant activity at the foliar level, which by preventing degradation processes prolongs life span of leaves and flowers. Trade-offs between benefits and costs of VOC emission as stress relief compounds are still not well understood as experiments with transgenic plants suggest that the metabolic cost for emitting isoprene (the most abundant VOC released from leaves) outweighs benefits [20][21].

Many ecological experiments have been designed with the aim of observing behavior of plants in wildlife conditions and get a comprehensive approach to the trade-off hypothesis. As an example, *Stryphnodendron adstringens* is a tree whose bark is used in Brazil as a source of medicinal tannins, nevertheless after bark harvesting, the tree generally dies. Tuller et al. in 2018 [22], in a manipulative field experiment, tested the hypothesis that harvesting leaves, which might serve as an alternative source of tannin, would be less detrimental for tree survival, growth, reproduction, and defense. Clipping the totality of leaves induced a trade-off such that reproduction (number of fruits) decreased but tannin concentration increased in plant tissues, as leaves were the highest defended tissue. These results are consistent with the hypothesis that damage induces higher secondary compound production to reduce the likelihood of subsequent herbivore damage[23]. In addition, investment in defensive compounds following herbivore attack instead of reproduction may be more profitable for long-lived trees, like *S. adstringens*, because they may have many future reproductive episodes[22].

3. Trade-Offs Lead to Physiological Changes upon Environmental Stimuli

Until now, we have dealt only with the basis of trade-offs at a molecular level, but we cannot forget that all signaling, and responses start with an environmental stimulus. The huge array of cell receptors has evolved to become the way as cells perceive their surroundings and interact with it. Then, once the stimuli are sensed and the responses given, what comes next? Well, for plants, as for other living organisms, is quite important to know if the given response was effective, so feedback processes must be established. Therefore, a changing environment is not healthy for plant development since it makes plants more susceptible to biotic and abiotic stresses. Environmental factors are also responsible of phenotype-shaping whose expression depends on the genes that have been activated by the transduced signal.

Temperature is one of the main factors intervening in tolerance responses to stress conditions, because such factor is always fluctuating along with the day, and changes abruptly with the seasons of the year. Furthermore, global climate change is showing a tendency to increasing temperature, and the understanding of the impact of this phenomenon on plants is a priority to mitigate the contemporaneous agriculture problems. In plants, temperature sensing is associated with fluctuations in membrane fluidity, histone modifications, activation of protein kinase cascades, and generation of ROS[24].

Rice plants infected with *Xanthomonas oryzae*, at elevated temperature, displayed upregulation of ABA biosynthesis and signaling genes, and downregulation of SA-responsive genes. Although, under the same conditions, rice plant carrying the *Xa7* gene exhibit resistance to this pathogen, suggesting that SA-independent defense signaling occurs at high temperature [25]. This fact shows that temperature is involved in the regulation of resistance genes expression upon pathogen attack and hormone crosstalk, since temperature accelerates breakdown in some plant-pathogen systems, though in some other cases it stimulates an enhanced response[2][26]. Similar behavior was observed in *Arabidopsis* exposed to *P. syringae*, where susceptibility was enhanced by increasing temperature. This effect is due to inhibition of SA-biosynthetic and SA-responsive gene expression, and upregulating genes involved in JA-mediated signaling and ABA biosynthesis, suggesting that an important interplay between SA and ABA/JA signaling is operating[27].

Extremes conditions of temperature affect negatively both the growth and defense processes as plants have to adequate transcriptional pathways and produce osmotic factors to avoid freezing. Cold stress stimulates membrane rigidification and cytoskeletal rearrangement. The cold signal is perceived by the membrane and temperature sensor (COLD1/RGA1) and other components, leading to an influx of Ca^{2+}, ROS production, ABA accumulation, and MAPK cascade (OsMKK6-OsMPK3) reaction[28]. Several studies lead us to believe that ROS are the key for understanding trade-offs under stress conditions, since at low concentration they trigger defenses and developmental responses at early stages, whereas at highest concentration they attack the cell membrane for destroying the cell under breakdown of the defense barrier[29][30]. The redirection of functions upon chilling stress is logically associated with the DNA damage that induces protective death of columella stem cell daughters leading to restoration of the aux-in maximum in the quiescent center (QC) and maintenance of functional stem cell niche activity in *Arabidopsis* roots. This breakthrough supports a new concept in which DNA damage and ROS production coordinate cell fate during responses to chilling stress[28][31].

Soil salinity is nowadays one of the most extended problems that agriculture is facing worldwide, it has been provoked by mankind irresponsible soil exploitation, and bad practices applied to extensive agriculture. This issue provokes significant economic losses because of its effects on plant metabolism, it causes a total disorder of growth regulators and uncoupling major physiological and biochemical processes [32]. Under salt stress the secretion of ET occurs, as it does under other types of stresses. Through ET burst, plants alert to other parts of itself and to its similar ones that it is under a harmful damage, so it can start up with stress responses. However, when the stress persists, it can trigger the initiation of senescence, chlorosis, and abscission processes, and ultimately lead to plant death [33]. Moreover, a recent research showed that lettuce plants exogenously treated with BRs and spirostanic synthetic analogs, reduced significantly the ET production in roots and shoots[34]. Furthermore, it has been shown that rice's seedlings growth under NaCl stress is significantly enhanced by treatment with BRs and its synthetic analogs[35][36][37][38]. Also pigment concentration increases and proline content decreases in leaves, as an evidence of adaptability to such stress conditions[39][40]. As BRs are so environmentally friendly, this result is an evidence of sustainable solutions to the salinity problems that affect almost the whole world today.

Biotic stress causes numerous losses in crops yearly. Both above- and belowground microbes may affect the growth-defense balance of plants. In ecology, the growth-defense hypothesis states that the faster the plant grows the greater the damages due to pathogen attacks are, and vice versa. Fast-growing species invest most of the available resources in plant growth rather than in defense mechanisms, whereas the opposite occurs in slower-growing species[41]. The majority of the tests designed to prove this hypothesis have been carried out with aboveground tissues and this behavior seems to be the norm[5][42][43][44][45]. Similar results have been reported for the existing relationship between belowground growth rate and soil biota effects (microbial fungi and bacteria) [18]. However, the established relationships suggests that belowground plants are involved on many interactions via their roots with antagonistic and mutualistic organisms[18]. Consequently, slower-growing species are benefitted from the soil mutualist at higher extent than faster-growing species. These studies demonstrate that GDT could be a complex regulator phenomenon which can be used as a predictor of plant community responses to pathogens.

An interesting fact, evidencing GDT-induced changes is that axial resin ducts, which are costly defensive structures, remain imprinted in tree rings of conifers, so they might become a valuable proxy to evaluate defensive investment. Vázquez-González et al. recently studied the responses to both spatial and temporal environmental variation in resin duct production, and to explore growth-defense trade-offs. To that aim, they applied dendrochronological procedures to quantify annual growth and resin duct production during a 31-year-period in a Mediterranean pine species, including trees from nine populations planted in two common gardens. Interestingly they found that annual resin duct production differed among populations of *Pinus pinaster*. Such variation in defensive traits can be logically expected as a proof of the optimization of resources provided by the ecosystem which is part of the processes for long-term evolutionary adaptation. Besides, they found a strong evidence of a physiological growth-defense trade-off at the phenotypic level, indicated by a negative correlation between annual basal area increment—feature associated with growth—and annual resin duct density. Climate conditions are strongly related with the above correlation since it is expected that growth-defense trade-offs are more likely to emerge under limiting environmental conditions determining physiological constrains. Populations that evolved under more favorable growth conditions showed stronger physiological defensive constraints. This can be explained by the fact that such populations were the most dissimilar in climate conditions to the sites where the trees were planted.

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