



Resolution of growth–defense conflict: mechanistic insights from jasmonate signaling

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Induced plant resistance depends on the production of specialized metabolites that repel attack by biotic aggressors and is often associated with reduced growth of vegetative tissues. Despite progress in understanding the signal transduction networks that control growth–defense tradeoffs, much remains to be learned about how growth rate is coordinated with changes in metabolism during growth-to-defense transitions. Here, we highlight recent advances in jasmonate research to suggest how a major branch of plant immunity is dynamically regulated to calibrate growth–defense balance with shifts in carbon availability. We review evidence that diminished growth, as an integral facet of induced resistance, may optimize the temporal and spatial expression of defense compounds without compromising other critical roles of central metabolism. New insights into the evolution of jasmonate signaling further suggest that opposing selective pressures associated with too much or too little defense may have shaped the emergence of a modular jasmonate pathway that integrates primary and specialized metabolism through the control of repressor–transcription factor complexes. A better understanding of the mechanistic basis of growth–defense balance has important implications for boosting plant productivity, including insights into how these tradeoffs may be uncoupled for agricultural improvement.

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Introduction

Plant growth rate and reproductive output are intimately linked to the availability of photoassimilated carbon and other vital resources obtained from the environment. These same resources, however, are also used to produce

defense compounds and physical structures that protect tissues from destruction by herbivores and pathogens. The notion that plant growth and immunity are antagonistically linked stems from the observation that elevated defense is commonly associated with growth inhibition and, of agricultural relevance, reduced yield. Given the importance of these traits for plant fitness in diverse environments, it is generally acknowledged that plants have evolved strategies to balance growth and reproductive output with the need for defense [1–3,4*]. A mechanistic appreciation of how growth and immunity intersect has important implications for understanding not only the diversity of defense strategies employed across the plant kingdom, but also for improving sustainable crop production.

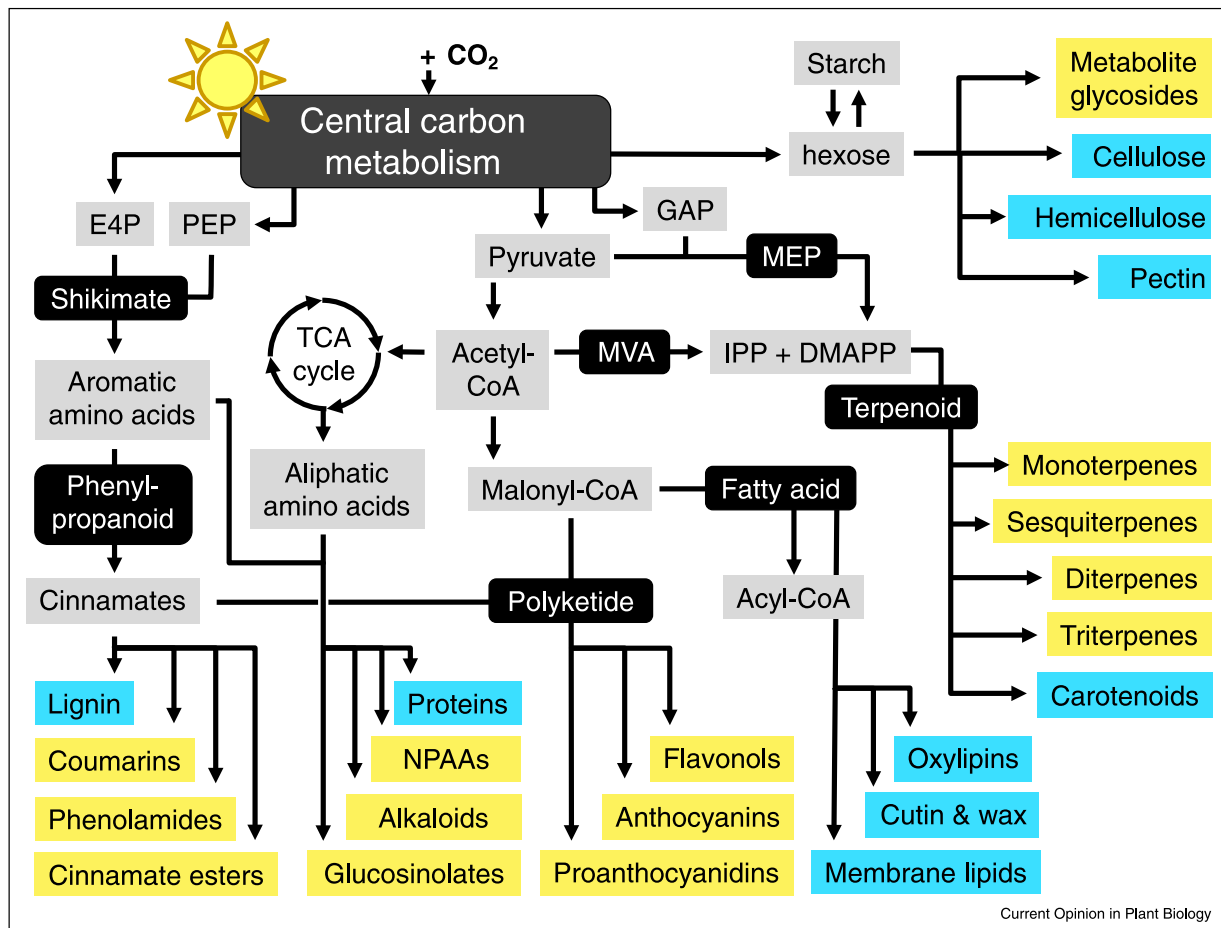
Significant progress has been made in understanding the molecular mechanisms of crosstalk between growth and immune signaling networks [5–8]. Although it is now clear that gene regulatory networks exert major control over growth–defense balance, a better understanding of the inherent conflicts between these major physiological tasks is needed to accurately predict genotype-by-environment interactions that give rise to tradeoffs [4*,9]. Hormone-based defense systems in which broad-spectrum resistance is conferred by induced expression of specialized defense proteins and metabolites, with associated growth suppression, provide attractive experimental systems in which to address the underlying mechanisms of growth–defense tradeoffs [7].

In this opinion article, we discuss growth–defense conflict from a mechanistic and metabolic perspective. We use the jasmonate signaling pathway to highlight how reprogramming of the interface between primary and specialized metabolism may be linked to changes in carbon availability and re-calibration of growth rate. We also propose a framework for understanding the modular architecture of the jasmonate signaling pathway in the context of opposing selective pressures associated with too much or too little defense, and how this signaling system integrates primary and specialized metabolism through control of repressor–transcription factor complexes. Finally, we consider how recent mechanistic insights into crosstalk between growth and immunity provide opportunities to uncouple growth–defense tradeoffs for agricultural benefit.

Jasmonate signaling reshapes the metabolic interface between growth and defense

Induced plant defense is associated with the production of a vast array of specialized metabolites (SMs) that

Figure 1



Connectivity between primary and specialized metabolism. Core metabolites (grey) in primary carbon metabolism (Calvin–Benson cycle, pentose phosphate pathway, glycolysis) are precursors for a variety of metabolic pathways (black boxes) that produce diverse primary (blue) and specialized (yellow) metabolites. Metabolic intermediates that are shared by primary and specialized metabolism illustrate potential for resource-based tradeoffs via competition between pathways. Defense-associated compounds in *Arabidopsis* include coumarins (e.g., scopoletin), cinnamate esters (e.g., sinapoyl malate), phenolamides (e.g., coumaroylagmatine), non-protein amino acids (NPAAs; e.g., N δ -acetylornithine), alkaloids (e.g., camalexin), glucosinolates (e.g., 4-methylthiobutyl-glucosinolate), flavonols (e.g., kaempferol glycosides), anthocyanins (e.g., cyanidin glycosides), proanthocyanidins (e.g., epicatechin polymers), monoterpenes (e.g., (*E*)- β -ocimene), sesquiterpenes (e.g., (*E*)- β -caryophyllene), diterpenes (e.g., rhizathalene), and triterpenes (e.g., thalianol). Not shown is the derivation of the polyamine moiety of phenolamides from aliphatic amino acids. Glycosylation (upper right) of metabolites, including coumarins, cinnamate esters, glucosinolates, flavonoids and terpenoids, serves multiple roles in defense. Whereas most alkaloids are derived from amino acids, some are generated from other precursors such as purines, terpenes, and polyketides. **Abbreviations:** E4P, erythrose-4-phosphate; PEP, phosphoenolpyruvate; GAP, glyceraldehyde 3-phosphate; TCA, tricarboxylic acid; MVA, mevalonate; MEP, methylerythritol 4-phosphate; IPP, isopentenyl pyrophosphate; DMAPP, dimethylallyl pyrophosphate.

mediate plant interactions with associated biota. Biosynthetic pathways for the major classes of SMs, including phenylpropanoids, polyketides, terpenoids, and nitrogen-containing compounds, are often regulated in an inducible fashion by jasmonate [10,11]. Because SMs are derived from one or more primary metabolites, induced production of SMs must be coordinated with corresponding changes in appropriate sectors of primary metabolism [12,13]. Pathways that highlight some of the major interconnections between specialized and primary metabolism in *Arabidopsis* are depicted in Figure 1. For example,

cinnamates generated by the phenylpropanoid pathway are precursors for monolignols and lignin production, as well as diverse phenylpropanoid and polyketide products. Large pools of proteinogenic amino acids are required for the biosynthesis of numerous defensive proteins that can accumulate to high levels in jasmonate-elicited tissues. Similarly, various amino acid precursors such as indole provide building blocks for nitrogen-containing SMs, including glucosinolates. As the largest and most diverse group of plant metabolites, terpenoids are produced from isoprene units and include primary metabolites (e.g.,

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