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EDITORIAL

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Trade-offs in plant responses to the environment

Plants respond to changing and variable environments with molecular and physiological changes that enable adaptation. Many of these responses depend on available energy pools which means trade-offs between prioritised processes are inevitable. The flexibility in these switches can influence plant success in responding to extreme weather events. Trade-offs are also important in the decision to establish symbioses between plants and microbes or mycorrhizae and in plant responses to insect or pathogen attack. The Special Issue 'Trade-offs in plant responses to the environment' (Plant, Cell and Environment 2023 Vol. 46;10) explores how plants 'decide' on where to best use energy and what those trade-offs mean for plant success, with measures of success ranging from computational models to end products.

As experimentalists, we often simplify our research design to changing individual environmental factors and investigating the mechanisms enabling the plant responses. To keep projects manageable we also often limit our research to subsections of whole plant development, physiology or molecular biology (e.g., focusing on roots, or shoots, or specific stages of development, at one or maybe two scales). However, plants exist in complex environments and have evolved complex ways to decide on processes such as resource allocation, whether that be for deciding the direction of growth, investing in secondary metabolites for defence or regulating stomatal conductance to control water use. The articles collated in this Special Issue evaluate functional trade-offs and explore whether or not one response occurs at the expense of another process.

Given the interactive nature of the processes, overlap between article topics is inevitable but they can be broadly separated into trade-offs in biotic and abiotic systems. Yet, the review by Leisner et al. (2023) highlights the complexity and importance of multistress interactions. They conclude that more work is needed to fill the knowledge gap that exists in understanding the interactions and trade-offs that occur when plants are exposed to combinations of biotic and abiotic stresses. We couldn't agree more and hope to see more work in this area in the future.

When presented with the idea of trade-offs, our first thought often relates to plant defence. Indeed, this is the field where trade-offs have been discussed the most. The typical expectation of plants growing under biotic stresses, is that to make defence compounds (i.e., secondary metabolites), resources for growth need to be killed. However, this generalisation often lacks nuance, a point we find developed in this special issue. A review from Malhotra et al. (2023) nicely details these nuances with examples where growth and defence occur as a trade-off and other times where growth and defence are synergistic. Additional research papers present further evidence of these complexities. In an updated view of the growth defence trade-off, Vega-Alvarez et al. (2023) use *Brassica oleracea* with differing resistance to *Xanthomonas campestris* to demonstrate that the immobilisation of sugars, rather than the cost of making secondary metabolites, is the cause of biomass loss. In contrast, Meline et al. (2023) looked at growth defence trade-offs in the context of tomato wilt disease (*Ralstonia solanacearum*). Studying both wilt resistant and susceptible lines, the authors show that wilt-resistant plants activate both growth and defence, while susceptible plants exhibited the expected trade-off between growth and defence. Thus, each plant−pathogen system has unique attributes, which reinforces the notion that there is no one-size-fits-all for growth defence trade-offs.

In addition to studies on pathogens, this Special Issue includes a series of articles on insect defence responses in plants. Again, we see examples for both, existence and absence of trade-offs. For example, Frost (2023) looked at the phytochemical profiles of trees from both an intact and a wound-inducible perspective. They found a trade-off between the diversity of phytochemicals from intact leaves and the diversity of induced phytochemicals in wounded leaves. In other words, plants with a high native phytochemical diversity had a lower inducible diversity, suggesting a trade-off between constitutive inducible defence abilities. In contrast, Guo et al. (2023) found no trade-off between growth and defence in corn borer resistant and corn borer susceptible maize inbred lines. Moving beyond the growth defence trade-off, Zhou et al. (2023) asked whether a rice DREB1A (dehydration-responsive element-binding 1A) line known to enhance abiotic stress tolerance would alter biotic resistance to a phloem-feeding herbivore. They confirm a trade-off exists with DREB1A expressing lines exhibiting reduced resistance to the brown planthopper (*Nilaparvata lugens*).

The articles highlighted thus far have focused on the detrimental plant biotic interactions. A fascinating different aspect of trade-offs in plant biotic interactions is included with the review by Mohd-Radzman and Drapek (2023) discussing trade-offs during symbiosis. This review covers the different degrees by which plants compartmentalise their symbionts and how this could be a strategy to mitigate risks. In summary, compartmentalising different endosymbionts separately helps avoid intraspecies competition between the symbionts and the subsequent reduced symbiont load. It also allows the host to maintain more control over symbiont physiology via resource delivery. This can be an important strategy when plants are growing in nutrient deficient conditions, controlling carbon investment to symbionts and ideally allowing selection for symbionts providing the best nutrient exchange.

This Special Issue also touches on trade-offs in the context of abiotic stresses, which is increasingly relevant for plant performance in a changing global climate. A review by Mao et al. (2023) highlights an important signalling pathway, the CBL-CIPK [CALCINEURIN B-LIKE PROTEIN (CBL)-CBL-INTERACTING PROTEIN KINASE (CIPK)], well-known for its role in regulating the crosstalk between growth and stress adaptation. In this review, the authors advocate for modulating the expression of different parts of the CBL-CIPK pathway to fine-tune and optimise the trade-off 'decision'.

In the context of hydraulic physiology, the interactions between carbon fixation and water loss constitute an important trade-off. Stefanski et al. (2023) show that warming and rainfall reduction makes stomatal behaviour more conservative in terms of water loss per unit carbon gain across 21 boreal and temperate tree species. Plants exhibit a typical 'recession' behaviour spending less when resources are limited. The authors predict increasingly conservative water-carbon trade-off behaviour in a warming drying world. In a set of simulations, Cai et al. (2023) suggest that the root hydraulic conductivity and/or root length can also contribute to stomatal physiological trade-offs. It will be interesting to explore how a more conservative water-carbon trade-off at the stomatal level will also impact on leaf cooling and energy budgets. On this point, Muller et al. (2023) show that plants can adjust their cooling mechanism to changing environmental conditions by optimising their aerodynamic resistance which is linked to evaporative cooling. Understanding these physiological trade-offs in the context of increasingly harsh environments is an exciting and active area of research.

As the exploration of trade-offs grows, there will be an increasing need for accessible and relevant experimental systems. Golan et al. (2023) describe one such system in wheat to study the trade-off of individual plant fitness and community performance. Additional innovation in experimental systems aimed at studying trade-offs at different scales and under different environmental conditions will be needed to drive this field forward.

In an excellent conversational and in-depth review, Robinson (2023) delves into a popular theory on how plants manage trade-offs on a global scale, the optimal partitioning theory (OPT). The article argues that plants do not have to trade-off resource allocation between roots and shoot, which is the foundation of the whole-plant OPT. Instead, Robinson proposes a more realistic model that treats plants as groups of semiautonomous modules, which can manage local trade-offs, thus, advocating for consideration of local responses as opposed to solely global responses.

Overall, this Special Issue brings together an exciting and diverse set of manuscripts, each detailing a unique aspect of plant trade-offs. Indeed, finding a common theme upon which to structure this editorial was quite the challenge. However, this diversity is inherent to the topic and highlights the broad excitement in the scientific community for exploring trade-offs. Generalising is never the answer in biology.

Erin E. Sparks[1]
Amanda Rasmussen[2]

[1]*Department of Plant and Soil Sciences, University of Delaware, Newark, Delaware, USA*
[2]*Division of Agriculture and Environmental Sciences, School of Biosciences, University of Nottingham, Sutton Bonington, UK*

Correspondence
Amanda Rasmussen, Division of Agriculture and Environmental Sciences, School of Biosciences, University of Nottingham, Sutton Bonington LE12 5RD, UK.
Email: Amanda.Rasmussen@nottingham.ac.uk

Erin E. Sparks, Department of Plant and Soil Sciences, University of Delaware, Newark, DE 19713, USA.
Email: esparks@udel.edu

ORCID

Erin E. Sparks http://orcid.org/0000-0003-1543-6950
Amanda Rasmussen http://orcid.org/0000-0002-9204-8030

REFERENCES

Cai, G., Carminati, A., Gleason, S.M., Javaux, M. & Ahmed, M.A. (2023) Soil-plant hydraulics explain stomatal efficiency-safety tradeoff. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14536

Frost, C.J. (2023) Overlaps and trade-offs in the diversity and inducibility of volatile chemical profiles among diverse sympatric neotropical canopy trees. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14594

Golan, G., Abbai, R. & Schnurbusch, T. (2022) Exploring the trade-off between individual fitness and community performance of wheat crops using simulated canopy shade. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14499

Guo, J., Liu, S., Jing, D., He, K., Zhang, Y., Li, M. et al. (2023) Genotypic variation in field-grown maize eliminates trade-offs between resistance, tolerance and growth in response to high pressure from the Asian corn borer. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14458

Leisner, C.P., Potnis, N. & Sanz-Saez, A. (2023) Crosstalk and trade-offs: plant responses to climate change-associated abiotic and biotic stresses. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14532

Malhotra, B., Kumar, P. & Bisht, N.C. (2023) Defense versus growth trade-offs: insights from glucosinolates and their catabolites. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14462

Mao, J., Mo, Z., Yuan, G., Xiang, H., Visser, R.G.F., Bai, Y. et al. (2023) The CBL-CIPK network is involved in the physiological crosstalk between plant growth and stress adaptation. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14396

Meline, V., Hendrich, C.G., Truchon, A.N., Caldwell, D., Hiles, R., Leuschen-Kohl, R. et al. (2023) Tomato deploys defence and growth simultaneously to resist bacterial wilt disease. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14456

Mohd-Radzman, N.A. & Drapek, C. (2023) Compartmentalisation: a strategy for optimising symbiosis and tradeoff management. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14553

Muller, J.D., Rotenberg, E., Tatarinov, F., Oz, I. & Yakir, D. (2023) Detailed in situ leaf energy budget permits the assessment of leaf aerodynamic resistance as a key to enhance non-evaporative cooling under drought. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14571

Robinson, D. (2023) OPT-ing out: root–shoot dynamics are caused by local resource capture and biomass allocation, not optimal partitioning. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14470

Stefanski, A., Butler, E.E., Bermudez, R., Montgomery, R.A. & Reich, P.B. (2023) Stomatal behaviour moderates the water cost of CO_2 acquisition for 21 boreal and temperate species under experimental climate change. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14559

Vega-Álvarez, C., Francisco, M., Cartea, M.E., Fernández, J.C. & Soengas, P. (2022) The growth-immunity tradeoff in *Brassica oleracea-Xanthomonas campestris* pv. campestris pathosystem. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14454

Zhou, S., Gao, Q., Chen, M., Zhang, Y., Li, J., Guo, J. et al. (2023) Silencing a dehydration-responsive element-binding gene enhances the resistance of plants to a phloem-feeding herbivore. *Plant, Cell & Environment*, 46. https://doi.org/10.1111/pce.14569