Received: 6 December 2023 | Accepted: 16 January 2024

DOI: 10.1002/ajb2.16294

American Journal of Botany

ON THE NATURE OF THINGS

Ontogenetic changes in ecophysiology are an understudied yet important component of plant adaptation

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KEYWORDS
adaptation, developmental timing, ontogeny, plant environmental response

Plants rely on adjustments in growth and development to respond to environmental stimuli. Developmental transitions, including germination, vegetative phase change, reproductive transition, and senescence, modify the growth patterns of plants and their requirements for survival. Consequently, the timing of developmental transitions and the developmental stage at which a plant encounters environmental stress hold significant implications for the performance of individuals, population dynamics, and community dynamics. If developmental phases, and the timing of transitions between them, are key to plant success in fluctuating environments, then understanding ontogenetic changes in plant environmental interactions is necessary to predict how plants will react to environmental stress and novel environments. Geneticists and molecular biologists have discovered many mechanisms governing developmental transitions, while developmental biologists have studied how plant form changes across ontogeny and ecologists have studied how plant form alters organismal interactions. However, there has been insufficient integration of these fields of study, hindering a comprehensive understanding of how plant development contributes to environmental adaptation and acclimation.

ALIGNING DEVELOPMENTAL PHASES AND ENVIRONMENT FOR OPTIMAL PLANT PERFORMANCE

Links among plant development, plant fitness, and ecosystem functioning lead us to hypothesize that selection on the timing of developmental transitions to align stress-tolerant developmental phases with periods of environmental stress is more prevalent than currently understood. Phase-specific differences in environmental tolerance could contribute to genotypic and species-specific adaptations to climate. As depicted in Figure 1, two genotypes (or species) labeled "A" and "B" exhibit different patterns of phase-specific stress tolerance throughout ontogeny. Depending on the environment (Env. 1 or 2) they inhabit, they will experience harsh environmental conditions at different times. Genotypes (or species) that align stress-tolerant developmental phases with periods of harsh conditions (e.g., genotype "A" in Env. 1) are thus expected to have increased fitness.

This example illustrates that the alignment between stress-tolerant developmental phases and harsh environmental conditions can arise through changes in developmental timing or ontogenetic alterations in plant growth and physiology. Despite considerable progress in our understanding of relationships between ontogeny and environmental response that support this hypothesis, knowledge of when developmental transitions occur and the extent of genetic variation in the timing of these transitions and phase-specific traits remains limited.

ONTOGENETIC DIFFERENCES IN ENVIRONMENTAL RESPONSE

As plants transition between developmental phases, their tolerance and response to environmental conditions changes (Figure 1). Plants in different developmental phases possess distinct organs (i.e., juvenile or adult leaves, flowers), access to

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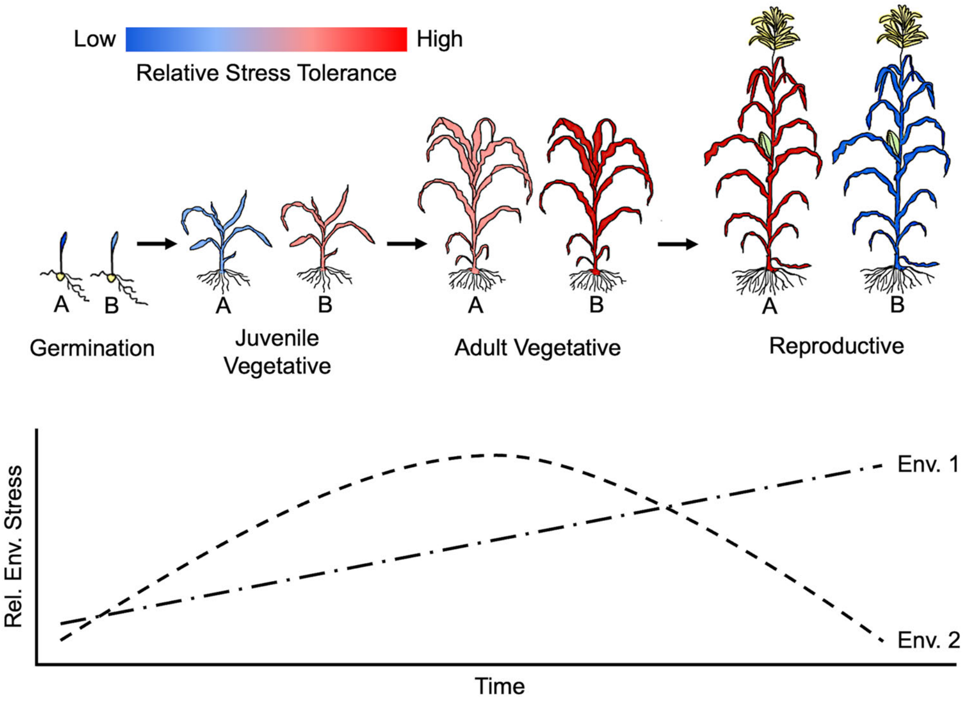

FIGURE 1 Diversity in stress tolerance between developmental stages and among individuals (labeled A and B) within a stage can result in selection on the timing of developmental transitions or phase-specific traits as levels of environmental stress change over time. Differences in stress patterns between environments can lead to local adaptation in these traits. The relative stress tolerance across development (i.e., phase-specific differences in physiology) and among individuals is denoted by color, with red indicating high tolerance and blue indicating low tolerance. Individuals A and B can represent different genotypes within a species or individuals between species of the same community. The lines Env. 1 and 2 on the graph represent different patterns of environmental stress across ecosystems.

resources, and physiological characteristics, which contribute to ontogenetic changes in environmental interactions. For example, during the transition from juvenile to adult vegetative phases, many plants produce different types of leaves that lead to shifts in carbon economics and suitability for different light environments. Juvenile leaves of multiple species are less costly to produce and have morphology and photosynthetic physiology better suited to low-light conditions, whereas adult leaves have a longer lifespan and have a morphology and physiology more profitable in high-light environments (Lawrence et al., 2022).

Furthermore, plants in different developmental phases possess unique genome-wide expression responses to environmental stimuli that control physiological responses. For example, during vegetative phase change, age-dependent increases in the expression of SQUAMOSA PROMOTER BINDING-LIKE (SPL) genes activate defense signaling genes, enhancing disease resistance during the adult vegetative phase in *Arabidopsis thaliana* (L.) Heynh. [Brassicaceae] (Hu et al., 2023). Additionally, there are phase-specific differences in gene expression responses to the environment, as observed in pre- and post-flowering *Sorghum bicolor* (L.) Moench [Poaceae] plants exposed to drought (Varoquaux et al., 2019). Developmental stage-dependent environmental responses can be so significant that different species at the same developmental stage exhibit more similar responses to environment than conspecifics at different stages (Parrish and Bazzaz, 1985). Although many published studies likely capture patterns of ontogenetic variation, failure to explicitly assess developmental stage may confound our ability to understand how plants interact with their environment across their lifespan, leaving a critical need for more research specifically focusing on phase-specific responses to environmental stress.

ENVIRONMENTAL IMPACTS ON THE TIMING OF DEVELOPMENTAL TRANSITION

The timing of plant developmental transitions is intricately responsive to environmental fluctuations (Bäurle and Dean, 2006). These plastic developmental responses are one of the most obvious plant responses to environment, noticeable even to casual observers. The most visually obvious transitions like flowering and senescence have long garnered the attention of humans, particularly in systems we depend on (e.g., crops) (Primack et al., 2009). Interactions between developmental timing and environment not only alter the duration of each developmental phase, but also determine the stage at which a plant experiences specific stresses. For instance, some plants accelerate flowering in response to drought, thereby shortening their growing season and escaping end-of-season droughts (Ludlow, 1989; Kooyers, 2015).

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Environmental impacts on developmental timing extend across multiple generations, increasing the likelihood of impacts on plant performance. For example, in *A. thaliana*, the flowering time of one generation influences the germination timing of the next, and vice versa (Burghardt et al., 2015). Additionally, temperature during seed set affects seed dormancy, such that, seeds set in autumn tend to exhibit stronger dormancy than those set earlier in the growing season. This is particularly evident in genotypes adapted to warmer climates, where mild winter temperatures fail to maintain primary dormancy throughout the winter (Iwasaki et al., 2022). While many studies have focused on environmental impacts on the timing of developmental transitions, there remains much unknown, especially regarding how multiple environmental factors and transitions interact and how complex fluctuations (e.g., precipitation in semiarid environments) influence developmental timing. Additionally, certain understudied developmental transitions, like the juvenile-to-adult vegetative transition known as vegetative phase change, continue to pose a significant knowledge gap that warrants further investigation.

DEVELOPMENTAL TIMING ALTERS ECOLOGICAL SELECTION

The timing of developmental transitions and ontogenetic differences in environmental response contribute to a plant's fitness and survival across ecosystems, affecting a population's persistence under current and novel environmental conditions. Evolution of phenology, especially leaf out and flowering time, are possibly the most well-known mechanisms of local adaptation in plants (Alberto et al., 2013). Studies show both genetic and plastic shifts in developmental timing within populations and communities in response to different environments, highlighting how such shifts affect individual performance across environments. An example of how selection of developmental transitions contribute to local adaptation is flowering time in *A. thaliana*, where researchers have found selection for either early or late flowering depending on environmental conditions (Korves et al., 2007). Furthermore, *A. thaliana* has apparently adapted to climates across its geographic range using strategies that cause different genotypes to germinate and flower at different times of the year to match when local conditions are favorable for these developmental phases (Exposito-Alonso, 2020; Martínez-Berdeja et al., 2020).

Developmental transitions can alter selection and affect population, community, and ecosystem dynamics. For example, during early development, fast-growing "ruderal" strategies are often selected for and as plants age, more competitive and stress-tolerant strategies prevail (Dayrell et al., 2018). Thus, plants in different developmental phases within the same ecosystem can deploy different growth strategies and changes in environmental conditions likely affect their performance in distinct ways. For instance, under water-stressed conditions, young *Artemisia californica* Less. [Asteraceae] plants maintain higher photosynthetic rates compared to older individuals however, these younger plants show greater drought sensitivity in other traits like stomatal conductance, whereas older plants are largely unaffected (Funk et al., 2021).

These differences in growth strategies and resource requirements likely contribute to ontogenetic changes in interactions with neighboring plants (Niinemets, 2004; Lasky et al., 2015). For instance, *Dioon sonorense* (De Luca, Sabato & Vázq.Torres) Chemnick, T.Greg. & Salas-Morales [Zamiaceae] seedlings are more shade tolerant than individuals at later developmental stages. This leads to increases in interspecific competition with neighbors as plants age, because the canopy cover from neighboring species shifts from facilitating seedling survival to creating a light-limited environment for adults (Álvarez-Yépiz et al., 2014). Ontogenetic changes in plant chemical and physical defense strategies alter competition with the non-plant community (e.g., herbivores) across development as well (Kariñho-Betancourt et al., 2015). As the timing of developmental transitions shifts in response to the environment, the developmental phase in which species interact with one another, and the duration of these interactions, are also likely to change, with consequences for individual performance (Yang and Rudolf, 2010). Due to the significance of how developmental transitions and phase-specific differences in environmental response contribute to a plant's fitness and survival across environments, more studies are needed to improve our understanding of the ecological implications of these responses.

FUTURE DIRECTIONS

Advancing knowledge of ontogenetic changes in ecophysiology and environmental response may yield better predictions of how plants cope with novel environments and shed light on potential adaptation in nature and breeding programs. As development represents a primary mechanism for sessile organisms to respond to environmental changes, we encourage researchers to intentionally consider plant developmental stages and transitions when designing experiments and constructing ecological and evolutionary models. Future studies that integrate molecular, organismal, and ecological research are needed to understand how the interactions among development, environment, and physiology contribute to plant fitness and ecosystem functioning, and how these interactions could provide insights for future agricultural and ecosystem management strategies.

AUTHOR CONTRIBUTIONS

E.H.L.-P. and J.R.L. both contributed to the conceptualization, writing, and revising of the manuscript.

ACKNOWLEDGMENTS

We thank Editor-in-Chief, Pam Diggle, for the invitation to write this essay and all reviewers for their thoughtful comments. The authors are supported by NSF IOS-2109780

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awarded to E.H.L.-P.; NSF DEB-1927009 and NIH R35GM138300 grants awarded to J.R.L.

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REFERENCES

Alberto, F. J., S. N. Aitken, R. Alía, S. C. González-Martínez, H. Hänninen, A. Kremer, F. Lefèvre, et al. 2013. Potential for evolutionary responses to climate change - evidence from tree populations. *Global Change Biology* 19: 1645–1661.

Álvarez-Yépiz, J. C., A. Búrquez, and M. Dovčiak. 2014. Ontogenetic shifts in plant-plant interactions in a rare cycad within angiosperm communities. *Oecologia* 175: 725–735.

Bäurle, I., and C. Dean. 2006. The timing of developmental transitions in plants. *Cell* 125: 655–664.

Burghardt, L. T., C. Jessica, E. Metcalf, A. M. Wilczek, J. Schmitt, and K. Donohue. 2015. Modeling the influence of genetic and environmental variation on the expression of plant life cycles across landscapes. *American Naturalist* 185: 212–227.

Dayrell, R. L. C., A. J. Arruda, S. Pierce, D. Negreiros, P. B. Meyer, H. Lambers, F. A. O. Silveira. 2018. Ontogenetic shifts in plant ecological strategies. *Functional Ecology* 32: 2730–2741.

Exposito-Alonso, M. 2020. Seasonal timing adaptation across the geographic range of *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* 117: 9665–9667.

Funk, J. L., J. E. Larson, and G. Vose. 2021. Leaf traits and performance vary with plant age and water availability in *Artemisia californica*. *Annals of Botany* 127: 495–503.

Hu, L., Q. Peng, A. Peper, F. Kong, Y. Yao, and L. Yang. 2023. Distinct function of SPL genes in age-related resistance in *Arabidopsis*. *PLoS Pathogens* 19: e1011218.

Iwasaki, M., S. Penfield, and L. Lopez-Molina. 2022. Parental and environmental control of seed dormancy in *Arabidopsis thaliana*. *Annual Review of Plant Biology* 73: 355–378.

Kariñho-Betancourt, E., A. A. Agrawal, R. Halitschke, and J. Núñez-Farfán. 2015. Phylogenetic correlations among chemical and physical plant defenses change with ontogeny. *New Phytologist* 206: 796–806.

Kooyers, N. J. 2015. The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Science* 234: 155–162.

Korves, T. M., K. J. Schmid, A. L. Caicedo, C. Mays, J. R. Stinchcombe, M. D. Purugganan, and J. Schmitt. 2007. Fitness effects associated with the major flowering time gene FRIGIDA in *Arabidopsis thaliana* in the field. *American Naturalist* 169: e141–e157.

Lasky, J. R., B. Bachelot, R. Muscarella, N. Schwartz, J. Forero-Montaña, C. J. Nytch, N. G. Swenson, et al. 2015. Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology* 96: 2157–2169.

Lawrence, E. H., C. J. Springer, B. R. Helliker, and R. S. Poethig. 2022. The carbon economics of vegetative phase change. *Plant Cell and Environment* 45: 1286–1297.

Ludlow, M. M. 1989. Strategies in response to water stress. *In* K. H. Kreeb, H. Richter, and T. M. Hinckley [eds.], Structural and functional responses to environmental stresses: Water shortage, 269–281. SPB Academic Publishing, The Hague, Netherlands.

Martínez-Berdeja, A., M. C. Stitzer, M. A. Taylor, M. Okada, E. Ezcurra, D. E. Runcie, and J. Schmitt. 2020. Functional variants of DOG1 control seed chilling responses and variation in seasonal life-history strategies in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* 117: 2526–2534.

Niinemets, Ü. 2004. Adaptive adjustments to light in foliage and whole-plant characteristics depend on relative age in the perennial herb *Leontodon hispidus*. *New Phytologist* 162: 683–696.

Parrish, J. A. D., and F. A. Bazzaz. 1985. Ontogenetic niche shifts in old-field annuals. *Ecology* 66: 1296–1302.

Primack, R. B., H. Higuchi, and A. J. Miller-Rushing. 2009. The impact of climate change on cherry trees and other species in Japan. *Biological Conservation* 142: 1943–1949.

Varoquaux, N., B. Cole, C. Gao, G. Pierroz, C. R. Baker, D. Patel, M. Madera, et al. 2019. Transcriptomic analysis of field-droughted sorghum from seedling to maturity reveals biotic and metabolic responses. *Proceedings of the National Academy of Sciences, USA* 116: 27124–27132.

Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters* 13: 1–10.

How to cite this article: Lawrence-Paul, E. H., and J. R. Lasky. 2024. Ontogenetic changes in ecophysiology are an understudied yet important component of plant adaptation. *American Journal of Botany*. e16294. https://doi.org/10.1002/ajb2.16294

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