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Research Progress on Plant Phenotypic Plasticity: Postprint

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Abstract

Phenotypic plasticity has emerged as a central concept in ecological evolutionary developmental biology, largely attributable to major contributions from plant plasticity research; however, the causes and consequences of phenotypic plasticity are still far from fully understood. From a holistic perspective, this review delineates the fundamental trajectory of phenotypic plasticity research development, introduces its research content, approaches, and brief history, and focuses on advances and future directions in several principal areas. The modern flourishing of plasticity research originated from a review on the evolutionary significance of plasticity, progressing from phenomenological descriptions and discussions of its genetic basis and the evolution of plasticity per se to explorations of underlying developmental mechanisms, plant growth and adaptive strategies, ecological impacts, and beyond. Future plasticity research should, on the basis of re-conceptualizing and re-evaluating phenotypic plasticity and its adaptiveness, devote greater attention to the complexity of environmental factors and plastic responses under natural conditions. The eco-evolutionary significance of phenotypic plasticity will continue to constitute a major focus of future investigations.

Full Text

Preamble

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Research on Phenotypic Plasticity in Plants: An Overview of History, Current Status, and Development Trends

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Abstract

Phenotypic plasticity has become a core concept in ecological evolutionary developmental biology ("eco-evo-devo"), due in large part to major contributions from plant plasticity research. However, the causes and consequences of phenotypic plasticity remain poorly understood. Herein, we summarize the development of phenotypic plasticity research from an integrated perspective, including research contents, approaches, and brief history, with a focus on research progress and future directions. Modern plasticity research is laid on the foundations of studies that delineated the evolutionary significance of plasticity in plants. We describe the phenomenon of plant plasticity and discuss its genetic basis and evolution before exploring the underlying developmental mechanisms, associated growth and adaptation strategies, and ecological consequences. Future plasticity studies should be based on understanding and evaluating phenotypic plasticity and its adaptability from a new perspective, with closer attention paid to the complex network of environmental factors and plastic responses that operate under natural conditions. We conclude that understanding the eco-evolutionary implications of phenotypic plasticity should remain the emphasis of future research.

Keywords: environmental complexity; modular trait; evolution of plasticity; adaptive plasticity; costs and limits; developmental plasticity

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Introduction

Phenotypic plasticity has emerged as a central theme in ecological evolutionary developmental biology, with plant studies making particularly significant contributions. Initially considered noise interfering with accurate genotype expression, both genotypic and phenotypic variation are now recognized as sources of evolutionary change following several seminal reviews [1-4]. Phenotypic plasticity—defined as the ability of a genotype to produce different phenotypes in different environments [1,10]—represents a crucial source of phenotypic variation. Plant research has been instrumental in advancing plasticity knowledge, from describing phenomena to exploring evolutionary mechanisms and ecological significance. These studies span multiple organizational levels and encompass diverse abiotic and biotic factors, linking plasticity concepts to growth strategies and adaptation theories, thereby establishing it as core content in the emerging field of eco-evo-devo [5]. Despite substantial progress, the causes and consequences of phenotypic plasticity remain incompletely understood [6], partly due to inconsistencies in fundamental aspects like quantification and adaptiveness [7-9]. While many articles focus on specific research areas, comprehensive overviews are lacking. Therefore, this review avoids exhaustive enumeration of studies and instead traces the developmental trajectory of plasticity research, examining mechanisms, ecological significance, and future trends to deepen understanding and promote plant plasticity research.

1. Research Content

Phenotypic plasticity refers to a genotype' s capacity to express different phenotypes across environments [1,10], also defined as the range of phenotypes a genotype can express under environmental influence [11] or an organism' s ability to alter phenotype in response to environmental cues [5]. Plasticity can be classified by various criteria: trait characteristics (e.g., stability, photoperiod), organismal performance in ecological contexts (e.g., predator avoidance, dispersal, resource acquisition), developmental timing (early [14] vs. late [15] sensitivity), reversibility [12] vs. irreversibility [13], and whether apparent plasticity stems from allometric relationships vs. true plasticity [16]. These categories are not mutually exclusive [17], and no classification can exhaustively capture all plastic phenomena.

Quantification methods are diverse. The most basic approach calculates mean trait differences across environments to assess environment-induced variation [18]. Many common formulas derive from ANOVA/ANCOVA analyses. Valladares et al. proposed relative distance plasticity indices and environmentally standardized plasticity indices, which show strong correlations with other metrics while offering greater sensitivity for interspecific comparisons [19]. Table 1 summarizes commonly used quantitative estimators of phenotypic plasticity.

2. Research Approaches

Plasticity research focuses on individual organisms and their phenotypic changes in specific traits, including both whole-plant and modular levels. Plants consist of reiterated, semi-autonomous structural and functional subunits (modules). Whole-plant plasticity represents the sum of environment-induced local module responses plus interactions from inter-module communication and behavioral integration. Different modular traits can exhibit vastly different local responses to the same environmental variation.

Early plasticity research primarily examined plant responses to single environmental factors or interactions between two factors under controlled or field conditions [34-36]. Abiotic factors included light, soil nutrients, and water; biotic factors included density, rhizobia, and microbes. Natural habitats present complex, temporally and spatially heterogeneous environmental influences whose effects depend on predictability, reliability, and organismal response time [37-38]. Recognizing this complexity remains a central challenge in plasticity research.

3. Research History

Phenotypic plasticity research originated with Woltereck's observations of Daphnia head height responses to nutrient levels [39]. The field developed slowly, partly due to population genetics theory emphasizing genotype-phenotype relationships [40-41]. Modern plasticity research was pioneered by Bradshaw' s evolutionary synthesis review [1], which sparked intense debates on whether plasticity itself could be a target of selection and whether "plasticity genes" exist—questions that remain contested. The rise of quantitative genetics and optimization theory catalyzed explosive growth in plasticity studies.

The emergence of developmental biology has added new dimensions, revealing molecular mechanisms underlying plasticity [42-43]. Research has shifted from describing variation to investigating developmental mechanisms, costs and limits of plasticity, and relationships between phenotypic integration and plasticity. Studies on plasticity' s role in evolution, species invasions, diversity, and distribution have progressed from theoretical hypotheses to empirical testing.

4. Genetic Mechanisms of Phenotypic Plasticity

Plasticity is genetically controlled through both genetic and epigenetic mechanisms [44]. Gene-level regulation involves structural genes (constitutively expressed with expression levels directly affected by environment) and regulatory genes (which mediate structural gene expression, such as transcription factors). Regulatory gene proponents argue that environmental information is converted into internal signals that activate different transcription factors, producing distinct phenotypes [47]. If regulatory gene activity is environmentally controlled, they can function as "plasticity genes," allowing plastic responses to evolve independently of trait means [23,45,48].

Epigenetic mechanisms also regulate plasticity, evidenced by transgenerational plasticity inheritance [49-50]. Bossdorf et al. integrated epigenetic case studies into ecological plasticity research [51], demonstrating that demethylation treatments significantly affect Arabidopsis flowering time, size at flowering, and biomass sensitivity to nutrient levels [52].

5. Developmental Mechanisms of Phenotypic Plasticity

Beyond genetic control, plasticity emerges from developmental self-regulation throughout the organism's lifecycle [5]. Through continuous interaction between developmental programs and environment, plastic responses involve physiological and morphological adjustments that are dynamic processes encompassing persistent environmental effects and internal signaling pathways [53]. This research has spawned the interdisciplinary field of ecological developmental biology (eco-devo), which examines how genome-environment interactions shape developing individuals and how adaptive developmental processes affect ecological and evolutionary dynamics [54].

Eco-devo aims to precisely determine how plants perceive and respond to real-world environmental variation [54-56], emphasizing the importance of incorporating natural environmental variation into developmental studies. Signal transduction pathways that coordinate molecular interactions to produce ecologically significant responses have attracted renewed interest [53,57-58].

6. Adaptiveness of Phenotypic Plasticity

Understanding adaptive plasticity is complicated by methodological disagreements and varying perspectives on genetic mechanisms and selection [8]. Plasticity' s adaptiveness depends on specific environments, species, and traits [59]; a plastic response adaptive in one context may be maladaptive in another [60]. Some trait responses enhance fitness, while others represent passive physiological or resource-limitation responses [16,38]. Single traits can simultaneously show multiple positive and negative trends to the same environmental factor [38].

Under natural conditions, plasticity reflects integrated organismal regulation—buffering, resisting, or promoting environmental influences [38]. The balance between positive and negative responses determines overall adaptiveness, which is highly variable [38,61]. Confusion between adaptiveness evaluation and cost assessment methods further complicates matters. Because controlled experiments exclude potential environmental selective forces, the overall adaptive significance of plasticity often remains uncertain [59]. Evaluating plasticity in natural populations is preferable [62].

[Figure 1: see original paper]

7. Costs and Limits of Phenotypic Plasticity

Related but distinct from adaptiveness, plasticity involves both benefits and costs [37-38]. Cost assessment methods correlate fitness with trait values and plasticity across environments using multiple regression models [11,37,63-64]. When trait values in one environment and differences between environments are both predictors, the partial regression coefficient for fitness on between-environment differences estimates plasticity costs (negative coefficients indicate costs) [65]. Empirical studies show costs are difficult to detect, possibly due to interactions and context-dependency [64,66-67]. Costs are only detectable when they exceed benefits.

8. Evolution of Phenotypic Plasticity

The view that plasticity has a genetic basis and can evolve independently of trait means is widely accepted [10,68]. Debates continue about whether natural selection can act directly on plasticity to enhance or maintain it [69-70] or whether recurrent environmental selection reduces adaptive plasticity [72-73]. Bradshaw, Simpson, and Baldwin defined conditions favoring or disfavoring plasticity, including directional, stabilizing, and disruptive selection [1]. Despite extensive theoretical work, experimental support remains limited, with most studies focusing on only two environments and lacking environmental breadth.

9. Evolutionary and Ecological Significance of Phenotypic Plasticity

Plasticity may be a potential macroevolutionary mechanism [7,74]. When environments change, organisms can shift phenotypes via plastic responses, preventing extinction. Through continuous phenotype-environment interactions, developmental system plasticity can accommodate such shifts through phenotypic and genetic adaptation (genetic assimilation) [75-76]. This hypothesis, while widely discussed [54], lacks comprehensive testing in natural populations.

Plasticity's role in diversification and speciation remains debated. It contributes significantly to establishment and spread of invasive plants [1,77-80], though evidence is mixed [81-85]. Plasticity aids colonization of new environments and responses to habitat changes, though it is not always necessary or sufficient [59]. Research on plasticity' s contribution to population dynamics under environmental change remains scarce, reflecting data limitations.

10. Future Directions

Although plasticity is considered a primary adaptive mechanism [86] and has been extensively studied, we remain far from fully understanding its causes and consequences [6]. Consensus is lacking on quantification methods and how natural selection affects reaction norms [7], and conclusions about adaptiveness and evolutionary significance are inconsistent [8-9].

Current quantification based on phenotypic differences fails to distinguish between environmental effects and organismal responses. Both plastic and stable phenotypes can reflect regulatory capacity—plasticity may represent successful active responses or regulatory failure, while stability may indicate either successful buffering or insufficient responsiveness [38]. Distinguishing environmental influence from organismal response is prerequisite for measuring adaptive capacity and evaluating costs. This separation also facilitates assessment of adaptiveness and costs.

Plasticity and its costs depend not only on specific modules and traits but also on trait correlations (phenotypic integration). Accurate assessment requires comprehensive evaluation of multiple traits' local responses and their integration. Natural environments involve simultaneous multiple factors, whereas controlled experiments typically examine single-factor responses, creating large gaps with real habitats [34,53].

Future research must better grasp environmental complexity through more realistic field experiments and multi-factor studies [53,87-89], examining environmental variation types, signal reliability, response speed, costs, and species-specific dependencies [1,33]. Plasticity studies should consider not only immediate inducing contexts but also environmental history, including triggering events and stress memory [6,85].

Research is expanding in both micro and macro directions. Microscopically, integrating genotypic and epigenotypic knowledge is crucial, with cell-level plasticity studies emerging [90]. Mechanistic explanations for signal perception, transduction, and phenotypic expression at molecular and cellular levels are needed [87]. Macroscopically, plasticity' s relationship with global climate change is gaining attention [11,91]. Most studies remain single-species focused, ignoring complex species interaction networks. Integrating plasticity concepts into multi-trophic relationships like food webs presents a major challenge.

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