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Received: 30 July 2024 | Accepted: 6 August 2024

DOI: 10.1002/ajb2.16395

SPECIAL ISSUE ARTICLE

American Journal of Botany

Doubling down on polyploid discoveries: Global advances in genomics and ecological impacts of polyploidy

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Abstract

All flowering plants are now recognized as diploidized paleopolyploids (Jiao et al., 2011; One Thousand Plant Transcriptomes Initiative, 2019), and polyploid species comprise approximately 30% of contemporary plant species (Wood et al., 2009; Barker et al., 2016a). A major implication of these discoveries is that, to appreciate the evolution of plant diversity, we need to understand the fundamental biology of polyploids and diploidization. This need is broadly recognized by our community as there is a continued, growing interest in polyploidy as a research topic. Over the past 25 years, the sequencing and analysis of plant genomes has revolutionized our understanding of the importance of polyploid speciation to the evolution of land plants.

KEYWORDS

allopolyploid, autopolyploid, polyploid, polyploidy, WGD, whole genome duplication

New insights and approaches to the study of polyploidy have led to exciting advances highlighted in this special issue of the *American Journal of Botany* and a companion issue of *Applications of Plant Sciences* (McKain et al., 2024), and a deeper exploration of polyploid biology in an increasingly global sample of plant study systems. In a previous special issue of the *American Journal of Botany* on polyploidy in 2016, we documented a nearly 4-fold increase in the percentage of talks at the annual Botany conference on polyploidy (Barker et al., 2016b). In this special issue, 8 years later, we revisit polyploid biology to bring together a collection of studies from across the spectrum of polyploid research to reflect on how far we have come in a relatively short time. Over the past 8 years, interest in polyploidy has continued to expand with a new series of meetings on polyploidy in organ development, repair, and disease (Roeder, 2019), which started in 2018 and merged with an existing polyploidy meeting series this past year (Pennisi, 2023) and in 2023, with local working groups that have started in different parts of the globe and held meetings like the Genome Evolution and Polyploid Symposium in South Africa. Starting in 2020 during the coronavirus pandemic, many researchers interested in polyploidy came together on a regular basis for the Polyploidy Webinar series that has to date featured over 60 different speakers from across the increasingly global polyploid community (Anon., n.d.). All of this activity and interest has propelled a dramatic increase in polyploid research.

Botanical fields have seen a number of significant advances in polyploid research that leverage genome data on previously unprecedented scale and quality and an improved analytical sophistication that enables a broader range of disciplines to engage in research on the biology of polyploidy. These advances include large-scale inferences of WGD across the plant phylogeny (Ren et al., 2018; One Thousand Plant Transcriptomes Initiative, 2019; Pelosi et al., 2022), polyploid phylogenetics (Rothfels, 2021; Hörandl, 2022; Morales-Briones et al., 2022; Xiong et al., 2022), in-depth analyses of the relationship between polyploidy and diversification (Landis et al., 2018; Zenil-Ferguson et al., 2019; Román-Palacios et al., 2020), and innovations to infer or date ancient WGDs (McKain et al., 2016; Clark and Donoghue, 2017; Thomas et al., 2017; Li et al., 2018; Tiley et al., 2018; Zwaenepoel and Van de Peer, 2019; Zhao et al., 2021; Sensalari et al., 2022; McKibben and Barker, 2023; Parey et al., 2023), and new metabolomic and proteomic research (Fasano et al., 2016; Gaynor et al., 2020; Alseekh et al., 2021; Sloan et al., 2024). At a more local level, insights into polyploid population genetics (Monnahan et al., 2019; Blischak et al.,

This article is part of joint special issues of the *American Journal of Botany* and *Applications in Plant Sciences*: "Twice as Nice: New Techniques and Discoveries in Polyploid Biology".

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2020, 2021, 2023; Bohutínská et al., 2021; Konečná et al., 2021; Conover and Wendel, 2022; Hämälä et al., 2024), adaptation to polyploid meiosis (Arter and Keeney, 2021; Bomblies, 2022; Morgan et al., 2022; Nibau et al., 2022; Gonzalo et al., 2023), polyploid biogeography and ecological niche (Gaynor et al., 2018a, b; Molina-Henao and Hopkins, 2019; Rice et al., 2019; Baniaga et al., 2020; López-Jurado et al., 2021; Padilla-García et al., 2022), coexistence of ploidies in environments (Laport and Ng, 2017; Sutherland and Galloway, 2017; Anneberg and Segraves, 2023; Anneberg et al., 2023a; Guo et al., 2023; Mortier et al., 2024; Segraves and Anneberg, 2024), and polyploids in a community context (Segraves, 2017; Gerstner et al., 2024b) have stimulated new research on the ecology of polyploids that has leveraged microcosms in the laboratory (Anneberg et al., 2023b; Castro et al., 2024) and work in the greenhouse, field, and urban environments (Wei et al., 2018; Forrester et al., 2020; Van de Peer et al., 2021; Van Drunen and Johnson, 2022; Mtileni et al., 2024). Not only have these research advances improved our understanding of polyploid biology, but the various community-driven engagements have also added new research dimensions to polyploid biology research.

Another notable change is the increased scope of polyploid research from nonmodel systems and researchers across the globe. Early research on polyploidy focused on a handful of well-studied plant systems that were concentrated in the northern hemisphere (e.g., Lutz, 1907; Winge, 1917; Clausen and Goodspeed, 1925; Müntzing, 1930, 1936; Babcock and Stebbins, 1938; Clausen et al., 1945; Stebbins, 1950; de Wet and Harlan, 1970; Harlan and DeWet, 1975; Levin, 1975, 1983). This classic work laid the foundation for understanding recent advances in the genetic, ecological, and physiological mechanisms underlying polyploid formation, establishment, and their subsequent global and local distributions (Ramsey and Schemske, 1998, 2002; Otto and Whitton, 2000; Baack, 2005a, b; Whitton et al., 2008; Ramsey, 2011; Soltis et al., 2014; Barker et al., 2016b; Kreiner et al., 2017; Rice et al., 2019). However, this northern-hemisphere-limited focus also contributed to gaps in our knowledge about global patterns in polyploid ecology and evolution. Efforts to reduce this gap are notable in the 79% increase in the number of papers published on polyploidy in the 2010s versus the 2000s in the *American Journal of Botany* (*AJB*) (Figure 1). One notable aspect of this expansion is the inclusion of a broader range of plant systems, increasingly enabled by researchers outside the northern hemisphere drawing attention to polyploidy in southern hemisphere plant groups and ecosystems (Zanella et al., 2011; Tacuatiá et al., 2012; Marinho et al., 2014; Reis et al., 2014; Gunn et al., 2015; Welker et al., 2015; Oberlander et al., 2016; Glennon et al., 2019; Lopes et al., 2020; Thomas et al., 2021; Becker et al., 2022). This expansion is also reflected in an increase in geographic diversity of researchers publishing on polyploidy in *AJB* over the last couple of decades (Figure 1). Specifically, the number of countries represented by authors publishing on polyploidy in *AJB* has increased from 37% in the 2000s ($N = 30$ countries) to the 2010s ($N = 41$ countries), and the number of papers with Global South researchers participating in polyploid research published in *AJB* has doubled in the last decade ($N = 7$ to $N = 13$).

The present special issue reflects the growth in polyploid research since the last special issue on the topic 8 years ago. The 17 papers in this issue cover topics ranging from metabolomics to genome duplications that facilitate cold climate distributions from authors in six countries. We have organized the present special issue into three thematic areas of polyploid biology to help with navigating the papers: polyploid formation and genomic consequences, polyploid events across time and space, and ecological consequences of polyploidy. In the following sections, we provide a brief



FIGURE 1 Global representation of polyploid papers published in *American Journal of Botany* by country of the corresponding author across two decades (2000–2009: blue circles, 2010–2020: orange triangles). The shape sizes indicate the number of studies published from that country.

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overview of the highlights of each paper as a guide for readers.

POLYPLOID FORMATION AND GENOMIC CONSEQUENCES

It has been well acknowledged that polyploid species are widespread and occur in many plant families. Some species have intraspecific variation in their cytotype, or even the ploidy level of their cells (Keeler, 1998; Fox et al., 2020). Typically, intraspecific ploidy levels are observed to be even-numbered, while odd-numbered ploidies, including triploidy ($2n = 3x$), are generally considered rare. Polyploidy can be broadly categorized into autopolyploidy and allopolyploidy (Barker et al., 2016a; Doyle and Sherman-Broyles, 2017), while the classification of ancient polyploidy has been challenging (Garsmeur et al., 2014). Given the increasing availability of genomic data, genetic changes following polyploidy, such as biased retention and sub- or neofunctionalization of these duplicate genomes, have been extensively studied (Mayfield-Jones et al., 2013; Buggs et al., 2014; Conant et al., 2014; Renny-Byfield and Wendel, 2014; Mandáková et al., 2017; Renny-Byfield et al., 2017; Defoort et al., 2019; Bayer et al., 2021; Hao et al., 2021; Li et al., 2021; Bird et al., 2023; Sloan et al., 2024). The consequences of polyploidy have been related to speciation, adaptation, and other broad evolutionary and ecological implications (Wood et al., 2009; Jiao et al., 2011; Mayrose et al., 2011; Wendel, 2015; Soltis and Soltis, 2016; Landis et al., 2018; Wu et al., 2020; Qi et al., 2021; Van de Peer et al., 2021). In this section, five studies contribute a better understanding of the association of dioecy and polyploidy, computational modeling of different cytotype frequencies, classification of autopolyploidy, homoeologous gene conversion, and adaptive evolution.

Osterman et al. (2024, this issue) propose a theoretical framework to track the previously contradictory results about the association of dioecy and polyploidy. They quantified the direction and magnitude of the polyploidy–dioecy relationship across genera and across species and identified a negative association between dioecy and polyploidy across genera in general. However, a positive relationship could also be weakly supported if the studied lineages only included few dioecious species. Blonder (2024, this issue) investigated the interesting dioecious species, quaking aspen (*Populus tremuloides*), which has both diploids and triploids but no tetraploids. Triploids are known to have low fertility and therefore are relatively rare in nature. They have provided a computational model to simulate how triploidy can be maintained in quaking aspen.

Although numerous polyploidization events have been identified in plants, classifying these events as autopolyploidy or allopolyploidy remains challenging. Lv et al. (2024, this issue) present an overview of previously proposed approaches including cytological methods, marker-segregation-based and genomics methods. They then mainly focused on how frequently polysomic inheritance has been reliably documented in autopolyploids and suggested that observations of polysomic inheritance can lead to relabeling of taxonomically allopolyploid species as autopolyploid. They also highlighted the complexity of polyploid origins and inheritance types and suggested a combination of molecular cytogenetics and genomics to understand the effect of chromosome rearrangements.

Polyploidy has led to acceleration of genomic modifications, especially for increasing gene content and reshaping genetic pathways. The biased retention pattern of gene duplicates could generate different evolutionary outcomes. Thomas et al. (2024, this issue) investigated salt and heavy metal tolerance in *Cakile maritima* and the possible role of gene duplications (duplicates derived from polyploid or tandem duplication) in tolerance genes. They also highlighted that these candidate genes may be applied in enhancing the stress tolerance of *Brassica* crops. Another interesting genomic change following polyploidy is homoeologous gene conversion. Conover et al. (2024, this issue) present a new analytical framework using an expanded phylogenetic sampling to re-examine putative homoeologous gene conversion events in allopolyploid cottons and found such events are uncommon in *Gossypium*. This study not only provided strong evidence for the evolutionary history of gene conversion in cottons, but also demonstrated how taxon sampling could lead to false positive discoveries about gene conversion events in established allopolyploids.

POLYPLOID EVENTS THROUGH SPACE AND TIME

Whether polyploid events are prevalent throughout evolutionary history and occur across the globe has excited botanists for decades (Clausen et al., 1945; deWet, 1980; Fowler and Levin, 1984, 2016; Rice et al., 2019). The implications of both ancient and recent polyploid events on the vast diversity and adaptability of plants are still understudied. A key component of understanding the fundamental implications of polyploid biology is to better understand how many times polyploid events have occurred (time) and where they occurred (space). The five studies collected here highlight considerations and implications for examining how polyploidy drives plant diversification, trait evolution, and distribution.

One exciting focus of polyploid research is to understand how often polyploid events occur within the angiosperm phylogeny. McKibben et al. (2024, this issue) demonstrated that topological uncertainty has implications for understanding where and how many polyploidization events have occurred through time. This highlights a need to consider the quality of the species tree when aiming to link these deep time events to more recent outcomes of polyploid lineages. Other authors in this special issue call attention to the data used for evaluating polyploidy within and among lineages.

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Xavier et al. (2024, this issue) used the Zingiberaceae as a study system to highlight that both genome size estimates and chromosome counts provide key information to better understand the role of genome evolution in plant evolution and trait diversification.

Where in the phylogeny and when during evolutionary history polyploid events occur may also drive potential hybridization events and influence the global distributions of plant species. For instance, Tseng et al. (2024, this issue) draw our attention to phasing alleles to explore the nuances of the hybridization events between lineages within clades that have deep divergences (~20 Mya or more), which can also lend insight into ecological shifts by plant lineages. To this end, where species in a clade are distributed on Earth may be a consequence of polyploid events in their evolutionary past. Feng et al. (2024, this issue) demonstrated this phenomenon in the cosmopolitan Caryophyllaceae where paleopolyploid events are likely key to enabling species to predominantly live in alpine-arctic habitats. Lastly, Hagen et al. (2024, this issue) call on more polyploid researchers to examine which came first in evolutionary time, polyploidization or latitudinal distributions, in an effort to better explain the underlying mechanisms of the latitudinal polyploid gradient.

This group of studies demonstrates the far-reaching implications of polyploid biology both through geographic or climatic space and through time. They also highlight the need for polyploid researchers to consider methodology when asking deeper questions about polyploid biology.

ECOLOGICAL CONSEQUENCES OF POLYPLOIDY

In this section, six studies collectively advance our understanding of how polyploids fit into ecological systems from the integrative metabolic and microbiome level to increasingly higher trophic level interactions. At the cellular level of the polyploid species, authors examined how metabolic efficiency (Milosavljevic et al., 2024, this issue) can help or hinder autopolyploid establishment, whereas others sought to untangle metabolomic changes that followed a genome duplication event (Wu et al., 2024, this issue). Milosavljevic et al. (2024) investigated the changes in metabolic efficiency after a whole-genome duplication to test whether these boosts enable improved establishment of the polyploid individuals. They found that even small boosts in metabolic efficiency facilitated an increase in a polyploid's ability to establish and invade a community effectively. In a novel evaluation of polyploid metabolomics, Wu et al. (2024) found that genome duplications led to a variable outcome of metabolite concentration in polyploid cells. These studies highlight the variability that polyploidy introduces to biological systems at a cellular level.

Polyploid species likely have myriad implications for interactions within an ecosystem from microbiome communities to herbivore-level interactions (Segraves, 2017). Previous polyploid ecology research has investigated plant–herbivore interactions in natural systems (e.g., Hull-Sanders et al., 2009), but new experimental work on duckweed neopolyploids demonstrates the implications of polyploidy on preference and performance of aphid herbivores (Assour et al., 2024, this issue). Such work highlights the utility of experimental designs that can further untangle polyploidy's effect on species interactions at a macrolevel. Stepping down through an ecosystem's trophic cascade, we showcase one of the first examples of how polyploidy can affect a plant's microbiome, where polyploidy immediately alters a plant's microbiome, and how bacterial and fungal communities change differentially (Anneberg et al., 2024, this issue). Further, groundbreaking research on polyploid plant–soil–microbe interactions suggests that soil microbes play an important role in polyploid establishment (Gerstner et al., 2024a, this issue). These studies on microlevel interactions have identified exciting, novel dimensions to the reach of polyploid biology.

Lastly, as polyploid species exist in a community, especially with their diploid progenitors or among multiple ploidy levels, examining abilities for coexistence is a key component to deepening our understanding of polyploid biology. For two groups of African polyploid species, researchers examine how their traits enabled these species to coexist (vaz de Sousa et al., 2024, this issue) or make the best of their environment (van Mazijk et al., 2024, this issue). Using the well-known genus *Oxalis*, vaz de Sousa et al. (2024) examined how multiple ploidy levels coexisted across a landscape and demonstrated that the individuals' traits were likely key to their coexistence, akin to unique evolutionary lineages. In the Cape Floristic region, genome size held the key to understanding how two enigmatic groups of sedges with different ecophysiological strategies coexist in a similar landscape.

These exciting ecological explorations into polyploid biology yield a common thread: lineage-, or genotype-specific effects followed a polyploidization event across micro- to macrolevel interactions. This consistent outcome underscores the utility and need for polyploid biology research to delve deeper into how polyploidization shapes not only the organism experiencing a whole-genome duplication event, but its interactions with all organisms around it, at every trophic level.

CONCLUSIONS

One of the challenges set out in the special issue on polyploidy 8 years earlier was the need for additional model systems and integrating seemingly disparate spheres of polyploid research. In this special issue, we have highlighted the advancement of phylogenetic and genomic analytical approaches along with ecological data via experimental studies that have incorporated multiple nonmodel study systems into polyploid biology research. Further, many of these studies integrated insight from multiple trophic levels with complementary genomic data. The studies underscore

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the need for integrated research to deepen our understanding of the implications of polyploidization events in plant evolution. The next challenge proposed to polyploid researchers is to bring these multifaceted approaches to a range of nonmodel polyploid systems in both hemispheres to gain insight into the mechanisms and implications of this fundamental component of plant evolution.

AUTHOR CONTRIBUTIONS

Michael S Barker: Conceptualization; Writing—original draft; Writing—review and editing. **Yuannian Jiao**: Conceptualization; Writing—original draft; Writing—review and editing. **Kelsey L Glennon**: Conceptualization; Writing—original draft; Writing—review and editing.

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How to cite this article: Barker, M. S., Y. Jiao, and K. L. Glennon. 2024. Doubling down on polyploid discoveries: Global advances in genomics and ecological impacts of polyploidy. *American Journal of Botany* 111(8): e16395. https://doi.org/10.1002/ajb2.16395

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