



•综述•

# 多倍体植物混合倍性种群的建立机制研究进展

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**摘要:** 基因组多倍化是物种形成和进化的重要驱动力, 几乎所有植物都经历过至少一次基因组加倍。然而, 由于多倍体植株比二倍体表现出更高的死亡率, 多倍化机制被认为是植物进化的“死胡同”。一些植物物种具有自然混合倍性种群, 即同一物种具有不同倍性, 这为揭示多倍体的进化机制提供了最佳途径。本文从基因组加倍形成多倍体植物开始, 综述了混合倍性种群的形成、建立与维持的研究进展, 探讨了多倍体适应自然环境的种群分化而形成多倍体物种的机制。研究自然混合倍性种群的倍性组成、重复基因的功能分化以及多倍体的生态位分化, 有利于明确混合倍性自然种群的生态适应与维持机理, 以及多倍体植物的进化机制。

**关键词:** 多倍体植物; 混合倍性; 种群; 基因组加倍; 少数细胞型排斥

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## The mechanism of constructing mixed-ploidy populations in polyploid species

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### ABSTRACT

**Background & Aims:** Polyploidization, the duplication of entire genomes, is a key driver in the processes of speciation and evolution, and almost all plants experience at least one whole-genome duplication (WGD). Because polyploid species have higher mortality ratio than diploid ones, the mechanism of polyploidization is considered a “dead-end”. However, some plant species exist in nature as mixed ploidy populations. These populations contain species that exist at different polyploidy levels and therefore provide the best opportunities to study the mechanisms of polyploidy evolution.

**Progresses:** Beginning with the origination of polyploid plants from WGD, I reviewed the progress on the formation, establishment and maintenance of mixed-ploidy populations in polyploid plants. I also discussed the mechanisms of polyploid speciation through the population divergence of polyploid plants adaption in a natural environment.

**Prospects:** Detection of the ploidy components, divergence of multi-copy genes, and niche differentiation of polyploids facilitate the understanding of ecological adaptation and maintenance of mixed ploidy populations and the evolutionary mechanisms of polyploid plants.

**Key words:** polyploid plants; mixed ploidy; populations; whole-genome duplication; minority cytotype exclusion

基因组加倍(whole-genome duplication, WGD)形成多倍体是植物进化的主要机制之一(Soltis et al, 2009; Eric Schranz et al, 2012)。几乎所有植物都经历了至少一次基因组加倍(Jiao et al, 2011), 大约

35%的维管植物是多倍体(Wood et al, 2009), 很多基因组研究都发现了古老的基因组加倍事件(The Brassica rapa Genome Sequencing Project Consortium, 2011; Ren et al, 2018)。多倍化还是物种形成的

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重要驱动力,例如十字花科植物中有大约一半是新多倍体(neopolyploids) (Hohmann et al, 2015)。然而, Mayrose等(2011)发现多倍体具有比二倍体更高的灭绝率和更低分化速率,大多数新形成的多倍体不能存活下来(Arrigo & Barker 2012; Soltis et al, 2014),因此认为多倍体是植物进化的“死胡同”。持这种观点的理由包括:多倍体基因组不稳定、有丝分裂和减数分裂不正常、少数细胞型排斥(minority cytotype exclusion, MCE)以及重复基因的有害效应等(Levin, 1975; Morgan et al, 2020),这些因素不利于多倍体的生存。另一种观点则认为,虽然早期的多倍体比二倍体有更高的灭绝速率,但是建立了稳定种群的多倍体则有利于植物的进化(Soltis et al, 2014)。

多倍化事件的发生原因可能是随机的,也有可能是受到特定环境变化事件或逆境等诱导发生的。例如,研究发现基因组加倍和古多倍体的形成时间与一些历史灭绝事件(如白垩纪-古近纪)高度吻合,推测古多倍体可能是由这些事件导致的(Van de Peer et al, 2017; Ren et al, 2018)。其原因有三:一是历史灭绝事件使得多倍体占据了二倍体的生态位(Van de Peer et al, 2017);二是古多倍体是植物在长期适应过程中无性繁殖的产物,地下或水下的无性繁殖体躲过了流星撞击地球导致的极端气候条件(Freeling, 2017);三是与减数分裂有关的基因大量突变富集产生未分裂的配子从而形成多倍体(Zhang et al, 2013; Freeling, 2017)。此外,一些生物和非生物胁迫引起的自然选择也是导致多倍体形成的原因之一(Doyle & Coate, 2019; Van de Peer et al, 2021)。实际上,有很多物种如猕猴桃、烟草、小麦、蕨类等存在多倍性自然种群(曾华等, 2009; Soltis et al, 2014; 梁思琪等, 2019),而且大约有16%的植物物种具有混合倍性(同一物种不同倍性) (Rice et al, 2015)。例如,在湖南雪峰山和贵州发现的野生中华猕猴桃(*Actinidia chinensis*)存在二倍体和四倍体,美味猕猴桃(*A. chinensis* var. *deliciosa*)存在四倍体、五倍体和六倍体,而且高倍性多分布于高海拔地区(曾华等, 2009; Li et al, 2010)。中华猕猴桃不同倍性杂交后发生倍性分离,用六倍体母本与二倍体父本杂交得到的子代群体中存在从三倍体到8倍体的多倍体(饶静云等, 2012)。

多倍体进化的机制是否为植物进化的驱动力?

即多倍体及其引起的物种形成是随机发生的巧合还是某些特定环境变化或灭绝事件的产物(Van de Peer et al, 2017; Wu et al, 2020)? 研究混合倍性物种的形成与维持机制为回答这些科学问题提供了重要思路(Kolář et al, 2017)。1938年, Babcock和Stebbins提出“多倍体复合体”(polyploid complex)的概念(Babcock & Stebbins, 1938)。Stebbins (1950)在 *Variation and Evolution in Plants* 一书中对多倍性复合体进行了详细讨论,并在 *Chromosomal Evolution in Higher Plants* (Stebbins, 1971)中提出多倍体复合体可以作为进化单元的观点,认为其可以为多倍体的进化研究提供准确可信的科学依据。

## 1 混合倍性种群的形成

自然界为什么存在混合倍性种群? 其中一个重要原因是新多倍体形成的速率高于灭绝速率(Kolář et al, 2017)。被子植物中有15%的物种形成事件起源于多倍体,而蕨类植物中这一比例达到31%(Wood et al, 2009)。新多倍体的形成机制主要包括未减数分裂的配子、体细胞加倍和杂交等(图1)(Zhang et al, 2019)。由于种群中新产生的多倍体频率较低,在随机交配体系中处于劣势,无法找到适

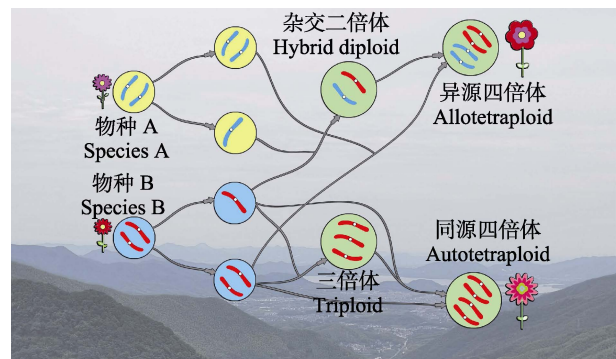


图1 多倍体形成途径的简单示意图。二倍体物种产生正常的单倍体配子和未减数分裂的配子,未减数分裂配子可以和单倍体配子产生三倍体,也可以融合产生同源四倍体;同时也可以通过体细胞加倍产生同源四倍体;异源四倍体通过物种之间未减数分裂配子的融合或者通过物种间的杂交再加倍产生。

Fig. 1 Formation paths to polyploid species. Diploid species produce normal haploid gametes and unreduced gametes. Unreduced gametes combine with haploid gametes to give rise to triploids or fuse to be autotetraploid species. Diploids can yield somatically polyploids. Allotetraploids are yielded through the fusion of unreduced gametes or the hybridization of haploid gametes from different species.

配对象,使其被排除在外而不能固定下来,这就是少数细胞型排斥假说(Levin, 1975)。该假说的另一种解释是不同倍性之间产生的新倍性后代(如三倍体)的适合度较低导致其不容易稳定建立种群(Kolář et al, 2017)。混合倍性种群的出现说明这些新倍性个体克服了这种少数细胞型排斥劣势,而且确实有研究发现稀有倍性个体并没有表现出适合度劣势(Kao, 2007)。

然而,目前仍不清楚这一少数细胞型排斥假说在形成自然混合倍性种群中有多大的作用。要克服少数细胞型排斥来形成新的多倍体种群主要有3种途径:一是不断形成新的多倍体并随机分布来提高新多倍体的频率;二是提高同一倍性内的交配频率而降低倍性间的交配频率;三是提高多倍体的竞争能力和繁殖能力从而弥补依赖频率的少数细胞型排斥劣势。从目前研究结果来看,繁殖力和可育性不能克服少数细胞型排斥,而且在稳定环境中多倍体的竞争能力也并不高于低倍体(Kolář et al, 2017)。但是有些研究结果发现多倍体在微环境、表型、授粉媒介和病菌侵染等的生态位分化有利于其克服少数细胞型排斥的影响(Ramsey & Ramsey, 2014; Kolář et al, 2017)。此外,由于种群间的不断迁入迁出以及人类干扰造成了空间异质性的微环境,有利于混合倍性种群的形成(Mráz et al, 2012; Kolář et al, 2017)。例如,混合倍性植物有65.0%的物种包含有奇数倍性的细胞型个体,这些混合倍性种群中大约有11.6%的个体是奇数倍性的细胞型(Kolář et al, 2017)。除了特定事件导致未减数分裂的配子和体细胞加倍,奇数倍性也可能是通过杂交形成的(Sabara et al, 2013)。稀有倍性个体的出现说明当地种群能频繁形成多倍体(Mandák et al, 2016)。这些奇数倍性和稀有倍性的出现说明自然种群中多倍体的形成经常以较高的速率出现(Ramsey & Schemske, 1998)。

## 2 混合倍性种群的建立与维持

多倍体形成之后能否稳定建群?首先,取决于其能否适应环境并成功生存下来。这个过程涉及重复基因的进化,而基因功能的分化是物种辐射的重要机制。多倍体更高的遗传变异和遗传多样性能有效缓冲重复基因的有害效应,通过亚功能化

(sub-functionalization)和新功能化(neo-functionalization)分化出更多的功能特性(De Smet et al, 2013; Zhang et al, 2019),使得多倍体比二倍体在环境适应性方面更具优势,能更适应极端环境(Fawcett et al, 2009; Rice et al, 2019; Van de Peer et al, 2021)。有些重复基因通过甲基化沉默其表达使其避免冗余基因造成的有害效应(De Smet et al, 2013)。多倍体也会增加物种的表型多样性(Nuismer & Cunningham, 2005)。然而,有研究发现多倍体比二倍体形成新种更慢且灭绝更快,使其多样化速率(即物种形成和灭绝的平衡)更低(Mayrose et al, 2011)。这可能是由于多倍体的多样化速率有滞后现象。实际上,基因组加倍常常导致更高的多样化速率(Suda et al, 2007; Van de Peer et al, 2017)。现存的有花植物大约25%–30%是新多倍体,即目前是多倍体但还没有经过重二倍化(re-diploidization,指多倍体亲本染色体经过重组与重排再形成二倍体的过程)形成新的物种(Suda et al, 2007; Van de Peer et al, 2017)。

其次,取决于其与二倍体亲本种之间的生态位分化。多倍体形成之后的生态位与二倍体亲本相比,有的更窄,有的更宽,更多的是占据二倍体亲本的生态位并与之重叠(Blaine Marchant et al, 2016)。这可能是由于多倍体植物比二倍体近缘种有更快的生态位分化速率(Baniaga et al, 2020)。多倍体和二倍体之间的生态位分化表现为生态位扩展或收缩,占据父母本的中间生态位以及开拓新的生态位等(Blaine Marchant et al, 2016; Castro et al, 2020)。而且在胁迫环境中,多倍体比二倍体更有优势,更能抵抗干旱、低温(Folk et al, 2020; Gunn et al, 2020; Wu et al, 2020)和病虫害(Hias et al, 2018; Wang et al, 2018)等胁迫。多倍体在胁迫环境中表现的这些抗性优势使其在与二倍体亲本的竞争中占据优势(Baduel et al, 2018; Van de Peer et al, 2021),并在胁迫环境中表现出更高的适合度和生存优势(Stevens et al, 2020)。而且,混合倍性种群能调节自然选择压力,增加分化选择压力,提高不同倍性个体之间的生态位分化。同域分布的多倍体之间的分化强于异域分布的多倍体(Nuismer & Cunningham, 2005; Sonnleitner et al, 2016),但是同域分布和异域分布的环境有明显差异。



### 3 混合倍性物种

为什么要选择混合倍性物种研究多倍体进化机制? 因为在混合倍性物种中能区分基因组加倍对物种表型、生态适应和基因组分化等方面的直接影响和间接影响。一般情况下, 现存的二倍体和多倍体之间的差异被认为是基因组加倍的直接影响, 但是基因组加倍后的选择压力也是二倍体和多倍体之间差异的重要原因。对近期自然形成的多倍体进行表型和基因组分析能评估基因组加倍的直接影响, 但来源于杂交的异源多倍体不能区分基因组加倍的最初影响, 而同源多倍体则没有基因组加倍的最初影响。而且混合倍性物种作为进化的中间环节, 可以反映多倍体的进化过程(Stebbins, 1971)。因为植物由低倍性到高倍性的进化趋势是基本共识, 因此可以利用多倍体复合体研究多倍体进化历史, 也可以通过杂交、物理或化学等实验手段进行人工诱导形成多倍体, 重演多倍体物种的形成过程。

基因组加倍后, 自然选择压力怎样影响多倍体植物的繁殖和适合度? 虽然多倍体植物借助更快的生态位分化来适应自然选择压力(Baniaga et al, 2020), 但是自然选择压力仍然可以通过影响基因连锁、亚基因组的重组以及基因功能分化、转座子(transposon elements)甲基化等影响多倍体植物的生存(De Smet et al, 2013; Bottani et al, 2018; Zhang et al, 2019; Wu et al, 2020)。这种影响受增加的染色体数量和基因数量影响, 而且同源多倍体和异源多倍体的影响机制不同。同源多倍体的基因连锁分析和异源多倍体的亚基因组重组分析能解析出自然选择影响多倍体植物的信号, 分析自然选择的影响途径(Yant et al, 2013; Zhang et al, 2013)。同源多倍体的染色体来自同一亲本基因组, 而异源多倍体来自不同的亲本基因组。所以分析在原生区形成的同源多倍体有利于明确基因组加倍的直接影响, 因为同源多倍体及其后代经历了相同的系统发育历史。

混合倍性物种有利于研究多倍体进化的机制和各个阶段, 包括多倍体的起源和形成、共存与分化等过程。因为混合倍性物种拥有独特的基因组和表型变化特征, 这些特征影响着物种的生态适应能力和种群之间的遗传分化(Kolář et al, 2017), 并可能导致新物种的形成, 特别是同域物种的形成

(Wood et al, 2009), 因为不同倍性之间容易导致生殖隔离(Rieseberg & Willis, 2007)。然而, 多倍体之间的生殖隔离程度弱于二倍体与多倍体之间的生殖隔离程度(Hülber et al, 2015), 这可能是由于多倍体形成合子之后的生殖隔离程度弱于二倍体(Sutherland & Galloway, 2017)。这种不完全的生殖隔离导致不同倍性之间发生基因交流, 减缓了多倍体的物种分化, 从而形成混合倍性种群。

### 4 展望

为揭示混合倍性物种的形成、建立与维持机制, 可研究野生混合倍性种群的组成及其多样性、未减数分裂配子和无性繁殖等对混合倍性种群形成的贡献、重复基因的功能分化、多倍体的生态适应能力及其生态位分化机理。明确混合倍性野生种群的起源、生态适应与维持机理, 有助于探讨多倍体植物的进化机制。

未来建议从以下几方面开展研究: (1)明确种群内部倍性多样性的分布格局, 对比分析不同地区野生种群的奇数倍性、优势倍性和稀有倍性的比例, 分析导致这种格局的成因, 验证少数细胞型排斥假说在混合倍性种群形成中的作用。(2)检测不同倍性群体的配子和无性繁殖个体, 明确未减数分裂的配子和无性繁殖对混合倍性形成的贡献; 区分新形成的多倍体和已经建立的多倍体, 以及是从二倍体不断产生新的多倍体, 还是多倍体形成后分化产生新的多倍体, 明确种群内的混合倍性形成机理。(3)野生混合倍性种群的维持机制研究, 从重复基因功能分化、性别变异、生态位分化分析混合倍性种群的维持机制, 以及分析温度、降水和土壤条件对混合倍性种群的影响, 分析气候和土壤等非生物因子的生态位分化对混合倍性种群维持的贡献。

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### 参考文献

- Arrigo N, Barker MS (2012) Rarely successful polyploids and their legacy in plant genomes. *Current Opinion in Plant Biology*, 15, 140–146.
- Babcock EB, Stebbins GL (1938) *The American Species of Crepis: Their Interrelationships and Distribution as Affected by Polyploidy and Apomixis*. Carnegie Institution of

Washington Publication, no. 504, Washington, USA.

- Baduel P, Bray S, Vallejo-Marin M, Kolář F, Yant L (2018) The “Polyploid Hop”: Shifting challenges and opportunities over the evolutionary lifespan of genome duplications. *Frontiers in Ecology and Evolution*, 6, 117.
- Baniaga AE, Marx HE, Arrigo N, Barker MS (2020) Polyploid plants have faster rates of multivariate niche differentiation than their diploid relatives. *Ecology Letters*, 23, 68–78.
- Blaine Marchant D, Soltis DE, Soltis PS (2016) Patterns of abiotic niche shifts in allopolyploids relative to their progenitors. *New Phytologist*, 212, 708–718.
- Bottani S, Zabet NR, Wendel JF, Veitia RA (2018) Gene Expression dominance in allopolyploids: Hypotheses and models. *Trends in Plant Science*, 23, 393–402.
- Castro M, Loureiro J, Figueiredo A, Serrano M, Husband BC, Castro S (2020) Different patterns of ecological divergence between two tetraploids and their diploid counterpart in a parapatric linear coastal distribution polyploid complex. *Frontiers in Plant Science*, 11, 315.
- De Smet R, Adams KL, Vandepoele K, Van Montagu MCE, Maere S, Van de Peer Y (2013) Convergent gene loss following gene and genome duplications creates single-copy families in flowering plants. *Proceedings of the National Academy of Sciences, USA*, 110, 2898–2903.
- Doyle JJ, Coate JE (2019) Polyploidy, the nucleotype, and novelty: The impact of genome doubling on the biology of the cell. *International Journal of Plant Sciences*, 180, 1–52.
- Eric Schranz M, Mohammadin S, Edger PP (2012) Ancient whole genome duplications, novelty and diversification: The WGD Radiation Lag-Time Model. *Current Opinion in Plant Biology*, 15, 147–153.
- Fawcett JA, Maere S, Van de Peer Y (2009) Plants with double genomes might have had a better chance to survive the Cretaceous-Tertiary extinction event. *Proceedings of the National Academy of Sciences, USA*, 106, 5737–5742.
- Folk RA, Siniscalchi CM, Soltis DE (2020) Angiosperms at the edge: Extremity, diversity, and phylogeny. *Plant, Cell & Environment*, 43, 2871–2893.
- Freeling M (2017) Picking up the Ball at the K/Pg Boundary: The distribution of ancient polyploidies in the plant phylogenetic tree as a spandrel of asexuality with occasional sex. *The Plant Cell*, 29, 202–206.
- Gunn BF, Murphy DJ, Walsh NG, Conran JG, Pires JC, MacFarlane TD, Birch JL (2020) Evolution of Lomandroideae: Multiple origins of polyploidy and biome occupancy in Australia. *Molecular Phylogenetics and Evolution*, 149, 106836.
- Hias N, Svara A, Keulemans JW (2018) Effect of polyploidisation on the response of apple (*Malus × domestica* Borkh.) to *Venturia inaequalis* infection. *European Journal of Plant Pathology*, 151, 515–526.
- Hohmann N, Wolf EM, Lysak MA, Koch MA (2015) A time-calibrated road map of Brassicaceae species radiation and evolutionary history. *The Plant Cell*, 27, 2770–2784.
- Hülber K, Sonnleitner M, Suda J, Krejčíková J, Schönswetter P, Schneeweiss GM, Winkler M (2015) Ecological differentiation, lack of hybrids involving diploids, and asymmetric gene flow between polyploids in narrow contact zones of *Senecio carniolicus* (syn. *Jacobaea carniolica*, Asteraceae). *Ecology and Evolution*, 5, 1224–1234.
- Jiao YN, Wickett NJ, Ayyampalayam S, Chanderbali AS, Landherr L, Ralph PE, Tomsho LP, Hu Y, Liang HY, Soltis PS, Soltis DE, Clifton SW, Schlarbaum SE, Schuster SC, Ma H, Leebens-Mack J, de Pamphilis CW (2011) Ancestral polyploidy in seed plants and angiosperms. *Nature*, 473, 97–100.
- Kao RH (2007) Asexuality and the coexistence of cytotypes. *New Phytologist*, 175, 764–772.
- Kolář F, Čertner M, Suda J, Schönswetter P, Husband BC (2017) Mixed-ploidy species: Progress and opportunities in polyploid research. *Trends in Plant Science*, 22, 1041–1055.
- Levin DA (1975) Minority cytotype exclusion in local plant populations. *Taxon*, 24, 35–43.
- Li DW, Liu YF, Zhong CH, Huang HW (2010) Morphological and cytotype variation of wild kiwifruit (*Actinidia chinensis* complex) along an altitudinal and longitudinal gradient in central-west China. *Botanical Journal of the Linnean Society*, 164, 72–83.
- Liang SQ, Zhang XC, Wei R (2019) Integrative taxonomy resolved species delimitation in a fern complex: A case study of the *Asplenium coenobiale* complex. *Biodiversity Science*, 27, 1205–1220. (in Chinese with English abstract)
- [梁思琪, 张宪春, 卫然 (2019) 利用整合分类学方法进行蕨类植物复合体的物种划分: 以线裂铁角蕨复合体为例. 生物多样性, 27, 1205–1220.]
- Mandák B, Vit P, Krak K, Trávníček P, Havrdová A, Hadincová V, Zákavský P, Jarolímová V, Bacles CFE, Douda J (2016) Flow cytometry, microsatellites and niche models reveal the origins and geographical structure of *Alnus glutinosa* populations in Europe. *Annals of Botany*, 117, 107–120.
- Mayrose I, Zhan SH, Rothfels CJ, Magnuson-Ford K, Barker MS, Rieseberg LH, Otto SP (2011) Recently formed polyploid plants diversify at lower rates. *Science*, 333, 1257–1257.
- Morgan C, Zhang HK, Henry CE, Franklin FCH, Bomblies K (2020) Derived alleles of two axis proteins affect meiotic traits in autotetraploid *Arabidopsis arenosa*. *Proceedings of the National Academy of Sciences, USA*, 117, 8980–8988.
- Mráz P, Španiel S, Keller A, Bowmann G, Farkas A, Šingliarová B, Rohr RP, Broennimann O, Müller-Schärer H (2012) Anthropogenic disturbance as a driver of microspatial and microhabitat segregation of cytotypes of *Centaurea stoebe* and cytotype interactions in secondary contact zones. *Annals of Botany*, 110, 615–627.
- Nuismer SL, Cunningham BM (2005) Selection for phenotypic divergence between diploid and autotetraploid *Heuchera grossulariifolia*. *Evolution*, 59, 1928–1935.

- Ramsey J, Ramsey TS (2014) Ecological studies of polyploidy in the 100 years following its discovery. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369, 20130352.
- Ramsey J, Schemske DW (1998) Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics*, 29, 467–501.
- Rao JY, Liu YF, Huang HW (2012) Analysis of ploidy segregation and genetic variation of progenies of different interploidy crosses in *Actinidia chinensis*. *Acta Horticulturae Sinica*, 39, 1447–1456. (in Chinese with English abstract) [饶静云, 刘义飞, 黄宏文 (2012) 中华猕猴桃不同倍性间杂交后代倍性分离和遗传变异分析. *园艺学报*, 39, 1447–1456.]
- Ren R, Wang HF, Guo CC, Zhang N, Zeng LP, Chen YM, Ma H, Qi J (2018) Widespread whole genome duplications contribute to genome complexity and species diversity in angiosperms. *Molecular Plant*, 11, 414–428.
- Rice A, Glick L, Abadi S, Einhorn M, Kopelman NM, Salman-Minkov A, Mayzel J, Chay O, Mayrose I (2015) The Chromosome Counts Database (CCDB)—A community resource of plant chromosome numbers. *New Phytologist*, 206, 19–26.
- Rice A, Šmarda P, Novosolov M, Drori M, Glick L, Sabath N, Meiri S, Belmaker J, Mayrose I (2019) The global biogeography of polyploid plants. *Nature Ecology & Evolution*, 3, 265–273.
- Rieseberg LH, Willis JH (2007) Plant speciation. *Science*, 317, 910–914.
- Sabara HA, Kron P, Husband BC (2013) Cytotype coexistence leads to triploid hybrid production in a diploid–tetraploid contact zone of *Chamerion angustifolium* (Onagraceae). *American Journal of Botany*, 100, 962–970.
- Soltis DE, Albert VA, Leebens-Mack J, Bell CD, Paterson AH, Zheng CF, Sankoff D, de Pamphilis CW, Wall PK, Soltis PS (2009) Polyploidy and angiosperm diversification. *American Journal of Botany*, 96, 336–348.
- Soltis DE, Segovia-Salcedo MC, Jordon-Thaden I, Majure L, Miles NM, Mavrodiev EV, Mei WB, Cortez MB, Soltis PS, Gitzendanner MA (2014) Are polyploids really evolutionary dead-ends (again)? A critical reappraisal of Mayrose et al (2011). *New Phytologist*, 202, 1105–1117.
- Sonnleitner M, Hülber K, Flatscher R, García PE, Winkler M, Suda J, Schönswetter P, Schneeweiss GM (2016) Ecological differentiation of diploid and polyploid cytotypes of *Senecio carniolicus sensu lato* (Asteraceae) is stronger in areas of sympatry. *Annals of Botany*, 117, 269–276.
- Stevens AV, Nicotra AB, Godfree RC, Guja LK (2020) Polyploidy affects the seed, dormancy and seedling characteristics of a perennial grass, conferring an advantage in stressful climates. *Plant Biology*, 22, 500–513.
- Stebbins GL (1950) *Variation and Evolution in Plants*. Columbia University Press, New York.
- Stebbins GL (1971) *Chromosomal Evolution in Higher Plants*. Edward Arnold, London.
- Suda J, Weiss-Schneeweiss H, Tribsch A, Schneeweiss GM, Trávníček P, Schönswetter P (2007) Complex distribution patterns of di-, tetra-, and hexaploid cytotypes in the European high mountain plant *Senecio carniolicus* (Asteraceae). *American Journal of Botany*, 94, 1391–1401.
- Sutherland BL, Galloway LF (2017) Postzygotic isolation varies by ploidy level within a polyploid complex. *New Phytologist*, 213, 404–412.
- The Brassica rapa Genome Sequencing Project Consortium (2011) The genome of the mesopolyploid crop species *Brassica rapa*. *Nature Genetics*, 43, 1035–1039.
- Van de Peer Y, Ashman TL, Soltis PS, Soltis DE (2021) Polyploidy: An evolutionary and ecological force in stressful times. *The Plant Cell*, 33, 11–26.
- Van de Peer Y, Mizrachi E, Marchal K (2017) The evolutionary significance of polyploidy. *Nature Reviews Genetics*, 18, 411–424.
- Wang WN, He YH, Cao Z, Deng ZN (2018) Induction of tetraploids in *Impatiens* (*Impatiens walleriana*) and characterization of their changes in morphology and resistance to downy mildew. *HortScience*, 53, 925–931.
- Wood TE, Takebayashi N, Barker MS, Mayrose I, Greenspoon PB, Rieseberg LH (2009) The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences, USA*, 106, 13875–13879.
- Wu SD, Han BC, Jiao YN (2020) Genetic contribution of paleopolyploidy to adaptive evolution in angiosperms. *Molecular Plant*, 13, 59–71.
- Yant L, Hollister JD, Wright KM, Arnold BJ, Higgins JD, Franklin FCH, Bomblies K (2013) Meiotic adaptation to genome duplication in *Arabidopsis arenosa*. *Current Biology*, 23, 2151–2156.
- Zeng H, Li DW, Huang HW (2009) Distribution pattern of ploidy variation of *Actinidia chinensis* and *A. deliciosa*. *Journal of Wuhan Botanical Research*, 27, 312–317. (in Chinese with English abstract) [曾华, 李大卫, 黄宏文 (2009) 中华猕猴桃和美味猕猴桃的倍性变异及地理分布研究. *武汉植物学研究*, 27, 312–317.]
- Zhang HK, Bian Y, Gou XW, Dong YZ, Rustgi S, Zhang BJ, Xu CM, Li N, Qi B, Han FP, von Wettstein D, Liu B (2013) Intrinsic karyotype stability and gene copy number variations may have laid the foundation for tetraploid wheat formation. *Proceedings of the National Academy of Sciences, USA*, 110, 19466–19471.
- Zhang K, Wang XW, Cheng F (2019) Plant polyploidy: Origin, evolution, and its influence on crop domestication. *Horticultural Plant Journal*, 5, 231–239.

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