

RESEARCH ARTICLE

Does competitive asymmetry confer polyploid advantage under changing environments?

Wen Guo¹  | Na Wei²  | Guang-You Hao³  | Shi-Jian Yang¹  | Zhi-Yong Zhu⁴  |
Yong-Ping Yang⁵  | Yuan-Wen Duan⁵ 

¹Yunnan Key Laboratory of Plant Reproductive Adaptation and Evolutionary Ecology, Institute of Biodiversity, School of Ecology and Environmental Science, Yunnan University, Kunming, Yunnan, China

²The Holden Arboretum, Kirtland, Ohio, USA

³CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, Liaoning, China

⁴Key Laboratory of Tibetan Environment Changes and Land Surface Processes, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, 100101, China

⁵Germplasm Bank of Wild Species, Institute of Tibetan Plateau Research at Kunming, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan, China

Correspondence

Na Wei

Email: nwei@holdenfg.org

Yong-Ping Yang

Email: yangyp@mail.kib.ac.cn

Yuan-Wen Duan

Email: duanyw@mail.kib.ac.cn

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Abstract

1. Competitive interactions drive critical ecological processes in plant communities. Yet, how competitive interactions are influenced by polyploidy that has a widespread incidence in plants remains largely unknown.
2. To evaluate the hypothesis of competitive asymmetry between polyploids and diploids, we competed tetraploid and diploid plants of perennial herbaceous *Chrysanthemum indicum* L. (Asteraceae) at different relative frequencies under contrasting soil water contents. We quantified the interaction intensity between competing plants of the same (intraploidy) and different ploidy levels (interploidy), and measured functional traits related to gas exchange and plant water use to understand the underlying mechanisms.
3. The stronger competitive effect of tetraploids on diploids than that of diploids on tetraploids provided evidence for the competitive asymmetry. As a stronger competitor, tetraploids were limited more by individuals of their own than by diploids. Such competitive asymmetry was not only maintained under reduced soil water content, but also translated into higher above-ground biomass of tetraploids. Tetraploids showed more resource-acquisitive traits than diploids under high soil water content and more resource-conservative traits under reduced soil water content. As such, the higher trait plasticity in tetraploids than diploids likely explained the competitive asymmetry.
4. **Synthesis.** These results elucidate the nature and magnitude of species interactions between polyploid and diploid plants under changing environments and the underlying mechanisms, and provide important insights into the prevalence and persistence of polyploid plants under a changing climate.

KEYWORDS

competition coefficient, competitive asymmetry, drought, functional traits, gas exchange, polyploidy, stress gradient hypothesis, water use efficiency

Wen Guo and Na Wei contributed equally.

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1 | INTRODUCTION

Competitive interaction and habitat filtering (e.g. imposed by stress) influence species distribution and community structure (Maire et al., 2012; Napier et al., 2016; Seabloom et al., 2003). These effects can be common during the evolution of polyploidy (or whole-genome duplication), which is a key feature of flowering plants and has a widespread incidence across numerous plant lineages (Jiao et al., 2011; Wood et al., 2009). During the evolution of polyploid plants, newly arisen polyploids are at a numeric disadvantage when competing with abundant, locally adapted parental diploids (Fowler & Levin, 1984, 2016; Levin, 1975; Schluter, 2001). To overcome such minority effects ('minority cytotype exclusion'; Levin, 1975), increased niche differentiation and competitive dominance over diploid progenitors are predicted to be important (albeit not prerequisite) for polyploid establishment and evolution (Fowler & Levin, 1984, 2016). Both conditions could lead to divergence in ecological niche and distribution between polyploids and diploids, as identified by species distribution modelling (López-Jurado et al., 2019; Marchant et al., 2016). Even in the cases of niche conservatism (e.g. Glennon et al., 2014), fine-scale spatial segregation among polyploids and diploids is often observed in nature (Akiyama et al., 2021; Kirchheimer et al., 2016; Mráz et al., 2022). As a result of evolution in allopatry or fine-scale spatial segregation in sympatry, it remains largely unknown whether established polyploids are competitively dominant showing fitness advantage relative to diploids across diverse environments (Collins et al., 2011; Rey et al., 2017; Thompson et al., 2015). This question is of critical relevance to understanding diploid and polyploid species distributions and range shifts under changing climates (Rice et al., 2019; te Beest et al., 2012).

Competitive interactions between polyploids and diploids can be complex. For instance, owing to genomic and phenotypic novelty and versatility/flexibility of polyploidy (Otto & Whitton, 2000; Ramsey & Ramsey, 2014; Soltis et al., 2016; Van de Peer et al., 2017; Wei et al., 2019, 2020), polyploids can be competitively dominant ('polyploid dominance') and the competitive effect of them on diploids ($\alpha_{2x,4x}$, 4x and 2x refer to tetraploids and diploids, respectively) is expected to be stronger than the effect of diploids on polyploids ($\alpha_{4x,2x}$; Figure 1a). As a result, polyploids may experience a higher reduction in fitness when competing with individuals of their own (intraploidy) than they do with diploid individuals (interploidy). In other words, polyploids could be limited more by intraploidy than interploidy competition ($\alpha_{4x,4x} > \alpha_{4x,2x}$; Figure 1b), whereas competitively inferior diploids could be limited more by interploidy than intraploidy competition ($\alpha_{2x,4x} > \alpha_{2x,2x}$; Figure 1b). However, if polyploidy leads to, for instance, genomic instability, slower metabolism or subgenome expression bias (Comai, 2005; Grover et al., 2012; Levin, 1983), polyploids may be competitively inferior to diploids and limited more by diploids ('diploid dominance': $\alpha_{2x,4x} < \alpha_{4x,2x}$, $\alpha_{4x,4x} < \alpha_{4x,2x}$, $\alpha_{2x,4x} < \alpha_{2x,2x}$; Figure 1c,d), or competitively similar to diploids with comparable interploidy versus intraploidy competition ('competitive symmetry': $\alpha_{2x,4x} = \alpha_{4x,2x}$, $\alpha_{4x,4x} = \alpha_{4x,2x}$, $\alpha_{2x,4x} = \alpha_{2x,2x}$; Figure 1e,f). While quantifying intraploidy versus interploidy competition is fundamental to understanding the magnitude and outcome of species interactions, few experimental studies have done so between polyploid and diploid competitors (Collins et al., 2011; Rey et al., 2017; Thompson et al., 2015).

Competitive interactions can be environment dependent (Aschehoug et al., 2016; Brooker, 2006; Ploughe et al., 2019; Zhang & Tielbörger, 2020). The stress gradient hypothesis (SGH;

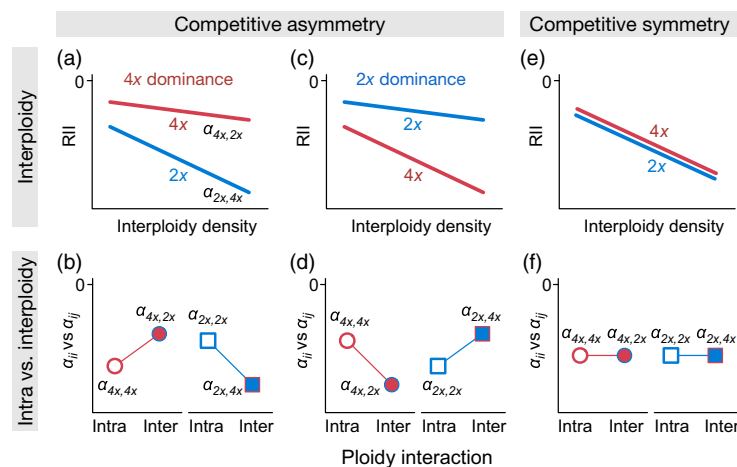


FIGURE 1 Hypotheses of competitive interactions between polyploids and diploids. (a–f) The competitive effect (slope) reveals interploidy competition between polyploids (4x, tetraploids as an example) and diploids (2x). Plant–plant interaction is quantified using the relative interaction index ($-1 \leq \text{RII} \leq 1$), with $\text{RII} < 0$ indicating competition. (a, b) If polyploids are stronger competitors than diploids (4x dominance), the competitive effect of polyploids on diploids ($\alpha_{2x,4x}$) is expected to be stronger than the competitive effect of diploids on polyploids ($\alpha_{4x,2x}$). Polyploids are also expected to be limited more by intraploidy competitive effect ($\alpha_{4x,4x}$) than interploidy effect ($\alpha_{4x,2x}$), whereas diploids are expected to be limited more by interploidy than intraploidy competitive effect ($\alpha_{2x,4x} > \alpha_{2x,2x}$). (c, d) If diploids are stronger competitors (2x dominance), the opposite patterns are expected: $\alpha_{2x,4x} < \alpha_{4x,2x}$, $\alpha_{4x,4x} < \alpha_{4x,2x}$, $\alpha_{2x,4x} < \alpha_{2x,2x}$. (e, f) In the case of competitive symmetry, interploidy and intraploidy competitive effects are expected to be similar: $\alpha_{2x,4x} = \alpha_{4x,2x}$, $\alpha_{4x,4x} = \alpha_{4x,2x}$, $\alpha_{2x,4x} = \alpha_{2x,2x}$.

Bertness & Callaway, 1994; Maestre et al., 2009) provides a framework for predicting how the magnitude of intraploidy and interploidy competitions change under environmental stress. The SGH predicts that competitive interactions weaken as the environment becomes more stressful, but the extent to which competition decreases or shifts to facilitation is influenced by other factors, such as stress type, fitness measure and characteristics of the interacting species (He et al., 2013). Plant interactions often shift from competitive to facilitative under increased non-resource stress (e.g. salinity, cold or heat) especially when assessed through survival, but often remain competitive with reduced intensities under increased resource stress (e.g. water, nutrient or light) especially when assessed through growth and reproduction (He et al., 2013). In the cases of increased resource stress (the focus of this study), the extent to which stress lowers competitive effects may differ between polyploids and diploids (Figures S1 and S2) if they exhibit different tolerance to stress. For instance, if polyploids are more stress tolerant than diploids, they are likely impacted less by stress and their competitive effect on diploids ($\alpha_{2x,4x}$) could be reduced less than the effect of diploids on polyploids ($\alpha_{4x,2x}$; polyploid dominance, Figure S1a), leading to enhanced competitive asymmetry with increased resource stress. By contrast, if diploids are more stress tolerant than polyploids, the opposite pattern is expected (diploid dominance under enhanced competitive asymmetry, Figure S1b). Alternatively, if polyploids and diploids respond similarly to stress, their competitive effects may be reduced by a similar magnitude (Figure S1c,d), leading to maintained competitive asymmetry with increased resource stress. While reduced competition is common under resource stress (He et al., 2013), the competitive effects of polyploids and diploids may not change (Figure S1e,f) if they are also limited by other factors (e.g. other limiting resources, space or neighbour density) or they exhibit different strategies or plasticities that do not alleviate competitive interactions in response to a resource stress. By contrast, if polyploids and diploids exhibit trade-offs between competition and stress tolerance, competitive asymmetry could be reduced or even reversed (Figure S1g,h). These hypotheses are yet to be tested for understanding how species interactions in polyploids and diploids respond to environmental stress (Rey et al., 2017; Thompson et al., 2015).

The divergence in functional traits that mediate responses to environments via phenotypic changes can influence the magnitude of competitive interactions in plants (Aschehoug et al., 2016; Gaudet & Keddy, 1988; Kraft et al., 2015). As polyploidy can alter the mean and plasticity of functional traits that influence plant fitness (Hao et al., 2013; Wei et al., 2019), trait divergence is expected to underlie the nature and magnitude of competitive interactions between polyploids and diploids. Maintaining competitive asymmetry or symmetry across environments, nevertheless, depends on the extent to which traits respond adaptively to changing environments (Wei et al., 2019). Under favourable conditions, competition favours an acquisitive strategy that can enhance resource consumption and carbon assimilation (Lorts & Lasky, 2020; Wei et al., 2019),

whereas under stressful conditions a more conservative strategy can be favoured for stress tolerance especially in perennial plants (Wei et al., 2019). For instance, polyploids may exhibit higher rates of gas exchange (net photosynthesis, stomatal conductance, transpiration rate) under low drought stress than diploids, which would promote plant growth (Vyas et al., 2007). Under high drought stress, polyploids could be more drought tolerant than diploids, due to, for instance, higher water use efficiency (WUE; Manzaneda et al., 2012) and xylem structure that permits water transport and photosynthesis under very negative water potential (Hao et al., 2013). Thus, examining functional traits across environments could provide critical insights for understanding the potential mechanisms underlying competitive interactions between polyploids and diploids.

To evaluate the competitive interactions between polyploids and diploids under changing environments (Figure 1; Figures S1 and S2), we competed diploid and tetraploid plants of a perennial herbaceous polyploid complex, *Chrysanthemum indicum* L. (Asteraceae), at different relative frequencies under two contrasting scenarios of soil water content. By quantifying intraploidy and interploidy competitive effects and a suite of functional traits related to gas exchange and plant water use, we aimed to address three core questions: (1) is there competitive asymmetry between polyploids and diploids with polyploids being competitively dominant? (2) how do intraploidy and interploidy competitive effects change under reduced soil water content? and (3) how do functional traits explain the competitive interactions between polyploids and diploids?

2 | MATERIALS AND METHODS

2.1 | Study system and sampling

The polyploid complex of *Chrysanthemum indicum* comprises two ploidy levels, diploid ($2x=18$ chromosomes) and tetraploid ($4x=36$) that likely have allopolyploid origins (Li et al., 2014). The diploids and tetraploids are morphologically similar, but tetraploids are relatively larger in plant and floral sizes (Figure 2). These perennial plants can reproduce both sexually by seed and asexually by rhizome (Shi et al., 2011). Such asexual reproduction is often more pronounced in tetraploids as they form large clusters of individuals compared to diploids that often grow singly (based on field observations). The diploid and tetraploid populations grow mainly in parapatry in China and often occur in open and dry habitats especially the tetraploids (Li et al., 2014). The tetraploids that likely experienced a geological period of drought during the Quaternary glaciation (Li et al., 2014; Yang et al., 2006) are more widespread than diploids (Figure 2). In their overlapping region in central China, the diploids and tetraploids are often spatially separated. Within this region in Shennongjia, China, we collected seeds from four diploid populations and six tetraploid populations (Figure 2; Table S1) in November 2015. Collecting permits were not required for *C. indicum*. Specifically, 3–10 plants were chosen at random in each population (Table S1) considering variation in population size.

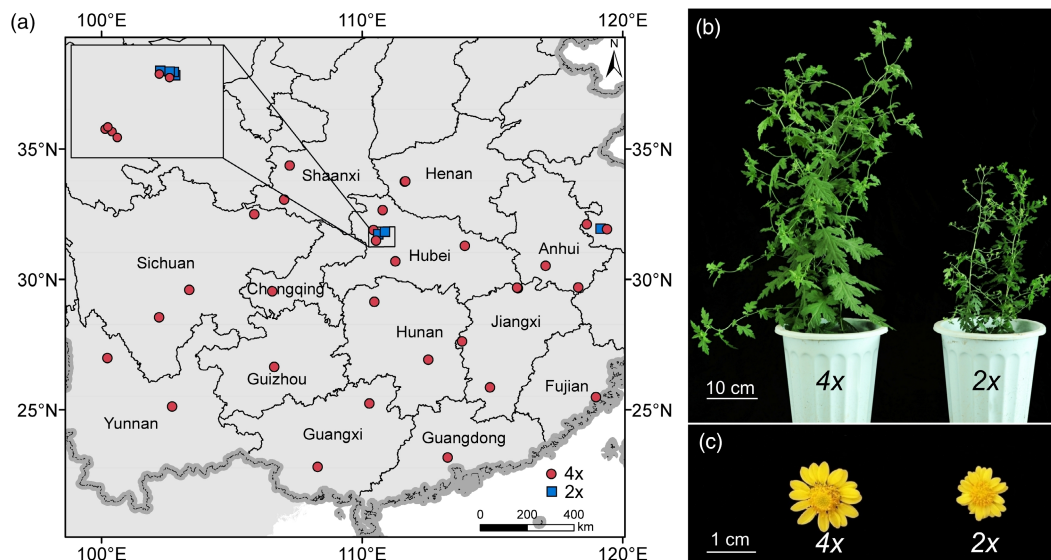


FIGURE 2 Distribution (a) and phenotype (b, c) of *Chrysanthemum indicum* polyplid complex in mainland China. The sampling area of this study is shown (the inner rectangle, a). The geographical locations of the tetraploid (4x) and diploid (2x) populations were from Li et al. (2014).

Then, from each individual, 5–10 flower heads were collected to obtain seeds and three fresh leaves were stored in moist plastic bags for verifying the ploidy levels using flow cytometry following a previous protocol by Guo et al. (2016).

2.2 | Seedling cultivation

In March 2016, seeds from different flower heads of the same maternal plant were pooled and sowed in peat substrates (0–10 mm; Novarbo) in 0.25-L pots. A total of 60 pots for the diploid populations and 72 pots for the tetraploid populations were used, with each pot containing c. 10 seeds from the same maternal family. Seedlings were grown under 25:15°C day:night temperatures and watered every other day in a naturally lit glasshouse at the Germplasm Bank of Wild Species (Kunming Institute of Botany). After 1 month, we harvested leaves from three seedlings of each pot to confirm seedling ploidy level using a flow cytometer. Pots with mixed ploidy levels ($N=8$ pots) were excluded from this study, which was likely due to dispersal when populations of the two ploidy levels grow close (Figure 2). In May 2016, seedlings of similar size (c. 5 cm in height) were used for the competition experiment and functional traits experiment at the same time.

2.3 | Competition experiment

To examine the effects of intraploidy and interploidy competitions, diploid and tetraploid seedlings were grown together at different relative frequencies (varying in 0, 2, 3 or 4 plants per ploidy level in each pot; Figure S3): 0:2, 0:3, 0:4, 2:0, 2:2, 2:3, 2:4, 3:0, 3:2, 3:3, 3:4, 4:0, 4:2, 4:3, 4:4. In this study, due to the concern of seedling mortality under a substantial reduction in soil water content (see

watering treatments below), we did not include a single diploid or tetraploid plant growing alone during the experimental setup. These 15 density combinations constituted the basic unit of the competition experiment (Figure S3) and were replicated 10 times, with 720 total plants in 150 7-L pots filled with 1.5 kg custom potting mixture (1:1, peat: perlite). To reduce potential confounding effects of maternal family and/or population-specific responses (Rosche et al., 2018; Wei et al., 2020) on competitive interactions, seedlings from different maternal plants and populations were mixed at random and transplanted for the competition experiment. Soil water content was maintained at field capacity ('FC'; 0.9 kg water per 1.5 kg potting mixture) by watering every 2 days for 3 weeks. On 1 June 2016, we started the watering treatments, with 5 replicates maintained at 80% FC and 5 replicates at 20% FC (referred to as 'normal watering' vs. 'reduced watering', respectively). To maintain the corresponding soil water content, pots were weighed every 2 days to record water loss and re-water accordingly, which was effective in maintaining the soil water content (Ma et al., 2010) when the weight of the matrix (soil and water) was much higher than plant biomass (kg vs. g). This experiment used a split plot design for the ease of watering, where watering treatments were assigned to whole plots with the replicated 15-density combinations randomized within the whole plots. Pots in the glasshouse were not rotated during the experiment due to the large size of the pots and fragile creeping stems under reduced watering. Thus, pot positions (i.e. column and row unique to individual pots in the glasshouse) were considered in data analyses later to account for the potential influence of variation in microenvironment conditions. The competition experiment was run for 2 months because (1) soil at 20% FC became very dry over the course of the experiment and plants already exhibited some leaf wilting (e.g. in diploids) and (2) we focused on growth rather than mortality-related responses in this experiment.

On 30 July 2016, we harvested the above-ground plant materials by ploidy level in each pot, but not the below-ground due to challenges in separating roots between diploid and tetraploid plants. Trials with diploid and tetraploid plants growing separately indicated similar root to shoot ratio between the ploidy levels (both ~1.0 under normal watering and 1.5 under reduced watering), and thus above-ground dry biomass is expected to correlate closely with whole plant dry biomass in both ploidy levels. The harvested plant materials were dried at 80°C for 72 h to obtain the above-ground dry biomass of diploid and tetraploid plants in each pot. Due to occasional plant mortality during the competition experiment, pots that did not match their original density combination ($N=10$) were excluded from data analyses.

2.4 | Functional traits experiment

We measured a suite of functional traits that are relevant to plant growth and drought tolerance (Table 1) in a separate experiment, to avoid potential influence of plant tissue collection on the competition experiment (Appendix S1). In the functional traits experiment, seedlings of the same ploidy level (i.e. two diploid or two tetraploid seedlings in a pot; Appendix S1) were transplanted with a total of 56 pots (112 seedlings) for each ploidy level. Ten 'empty' pots filled with the same potting mixture but no seedlings were included for

measuring evaporation. As in the competition experiment, on 1 June 2016, half of the experimental ($N=28$ pots per ploidy level) and 'empty' pots ($N=5$) were assigned at random to the normal watering treatment (80% FC) and half to the reduced watering treatment (20% FC) for 2 months. No seedling mortality occurred during this experiment.

Functional traits were measured primarily at the end of the experiment during 20–30 July 2016. Instantaneous gas exchange (maximum photosynthesis rate, A_{\max} ; stomatal conductance, g_s ; transpiration rate, E) was measured for a random subset of 13 pots per ploidy level per treatment using a LI-6400 portable photosynthesis system (LI-COR). Measurements were taken on a fully expanded green leaf from one plant of each pot between 09:30 and 12:00 h at a saturating irradiance ($1200 \mu\text{mol m}^{-2} \text{s}^{-1}$). The cuvette CO_2 concentration was maintained at $400 \mu\text{mol mol}^{-1}$. Relative humidity and leaf temperature were maintained at 50%–60% and 20–25°C, respectively. Instantaneous WUE (WUE_i) was calculated as A_{\max}/E .

From the same subset of pots used for gas exchange measurements, 10 pots per ploidy level per treatment were selected for determining leaf mass per unit area (LMA) and relative water content (RWC). Specifically, the largest, fully expanded green leaf from one plant in each pot was excised and weighed immediately for fresh mass. The leaf was scanned and leaf area was estimated using ImageJ v1.45 (Schneider et al., 2012). The same leaf was then submerged in distilled water overnight to obtain the saturated mass, and

TABLE 1 Key functional traits.

Traits	Definition (unit)	Description
Maximum photosynthesis rate (A_{\max})	Photosynthetic rate under light-saturated condition ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)	A_{\max} represents the maximal photosynthetic capacity. A_{\max} often correlates positively with biomass production and growth rate
Transpiration rate (E)	Loss of water from leaves in the form of vapour ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)	E is regulated by stomata and correlates with stomatal conductance. High E enables water flow to different plant parts including leaves for carrying out photosynthesis
Stomatal conductance (g_s)	The flux of CO_2 and water vapour through stomata ($\text{mmol m}^{-2} \text{s}^{-1}$)	g_s influences photosynthesis. High g_s allows more CO_2 diffusion into the leaf and water vapour exiting via transpiration
Total water use (TWU)	Plant water transpiration during the experiment (kg plant^{-1})	TWU reflects the total amount of transpiration during the period of plant growth. High TWU indicates strong water requirement of plants
Leaf mass per unit area (LMA)	Leaf dry mass per unit area (mg cm^{-2})	LMA reflects the thickness and/or dry mass content of leaf tissue. Low LMA permits high photosynthesis rate
Instantaneous water-use efficiency (WUE_i)	Ratio of photosynthesis (A_{\max}) to transpiration rate (E) ($\mu\text{mol mmol}^{-1}$)	WUE_i or photosynthetic WUE reflects the rate of carbon assimilation relative to the rate of transpiration. High WUE_i can result from increased carbon gain or reduced transpirational water loss
Long-term water-use efficiency (WUE_L)	Ratio of dry biomass accumulation to total water use (TWU) (g kg^{-1})	WUE_L reflects total dry biomass produced per unit water consumption. High WUE_L indicates high whole plant water use efficiency
Carbon isotope composition ($\delta^{13}\text{C}$)	Ratio of ^{13}C to ^{12}C in plant sample (‰)	$\delta^{13}\text{C}$ reflects photosynthetic WUE integrated over the life span of a leaf. High $\delta^{13}\text{C}$ indicates high integrated WUE
Leaf water potential (Ψ_{predawn})	Leaf water status during the predawn hours (MPa)	Ψ_{predawn} reflects the tendency of water movement. More negative Ψ_{predawn} is more likely to drive water column from soil to roots
Leaf relative water content (RWC)	Water content of leaf relative to full hydration (%)	RWC reflects plant water status. Species that are more drought tolerant can cope with lower RWC

Note: References for trait functions: A_{\max} (Murchie et al., 2009); E (Kramer & Boyer, 1995); g_s (Wong et al., 1979); TWU (Ma et al., 2010); LMA (Reich et al., 1997); WUE_i (Farquhar & Richards, 1984); WUE_L (Wright et al., 1988); $\delta^{13}\text{C}$ (Farquhar & Richards, 1984); Ψ_{predawn} (Sperry et al., 2002); RWC (Lambers & Oliveira, 2019).

dried at 80°C for 48 h for dry mass. LMA was calculated as leaf dry mass/leaf area, and RWC was calculated as (fresh mass – dry mass)/(saturated mass – dry mass) × 100. In addition, one mature leaf was collected at 06:00 h from each pot (8 pots per ploidy level per treatment) for measuring predawn leaf water potential (Ψ_{predawn}) using a WP4C Dewpoint Potential Meter (METER Group, Inc.). Another mature leaf was collected and dried for measuring carbon isotope composition ($\delta^{13}\text{C}$, ‰) using an isotope mass spectrometer (Thermo Finnigan MAT GmbH) at the Institute of Tibetan Plateau Research.

Plant total water use (TWU) and long-term WUE (WUE_L) were measured in a different subset of 10 pots per ploidy level per treatment, to avoid the influence of destructive leaf collection. As the experimental and ‘empty’ pots were weighed every 2 days to record water loss (for maintaining soil water content), TWU in each pot was determined as the difference between accumulated water loss in each experimental pot (transpiration and evaporation) and the average accumulated water loss per empty pot (evaporation). Plant TWU was estimated as the average TWU in each pot. To determine WUE_L , plants in each pot were harvested for estimating dry biomass (including both below-ground and above-ground). WUE_L was calculated as the ratio between plant dry biomass and TWU (Ma et al., 2010).

2.5 | Statistical analyses

The competitive interaction between plants was quantified using the relative interaction index, RII (Armas et al., 2004): $\text{RII} = (B_w - B_o) / (B_w + B_o)$, where B_w and B_o are the plant biomass with and without competitors, respectively. RII ranges between –1 and 1, with $\text{RII} < 0$ indicating competition. In this study, B_w was the average above-ground plant biomass of diploids or tetraploids in each pot. B_o was calculated as the average above-ground biomass (with one intraploidy competitor present) across replicated pots for diploids and tetraploids separately under each watering treatment, due to the absence of a single plant growing alone (see above). By doing so, our estimate of RII was conservative. To ensure the robustness of the findings, we also quantified interactions based on plant biomass directly (described below), which yielded consistent results as using RII (Supporting Information).

To test for competitive asymmetry between ploidy levels, we performed a general linear mixed model (LMM) with RII as the response variable using the package lme4 (Bates et al., 2015) in R v3.6.2 (R Core Team, 2019). The predictors included ploidy (2x or 4x), watering treatment (normal vs. reduced), intraploidy density (2, 3, 4 plants per pot) and interploidy density (0, 2, 3, 4), as well as their two-way and three-way interactions (Table S2). The random effects included pot positions (column and row) in the competition experiment to account for microenvironment variation and the fact that diploid and tetraploid plants grew together in the same pots (Figure S3) as column and row were unique to individual pots. We did not consider source populations in the random effects, because seedlings from different populations were mixed at random in the competition experiment. We also assessed competitive asymmetry using natural

log transformed above-ground dry biomass as the response variable while keeping the predictors and random effects the same as in the LMM of RII (Table S3). Statistical significance (type III sums of squares) and least-squares means (LS means) of predictors were assessed using packages lmerTest (Kuznetsova et al., 2017) and emmeans (Lenth, 2019). The slopes of interploidy density and intraploidy density in the LMM represented respective competitive effects (i.e. $\alpha_{4x,2x}$ and $\alpha_{2x,4x}$ for interploidy effects and $\alpha_{2x,2x}$ and $\alpha_{4x,4x}$ for intraploidy effects). The significance of interploidy density–ploidy interaction indicates competitive asymmetry between diploids and tetraploids. To further evaluate how competitive effects change under reduced soil water content and whether competitive asymmetry is maintained, interploidy competitive effect ($\alpha_{2x,4x}$ or $\alpha_{4x,2x}$) was compared between the normal and reduced watering treatments using planned contrasts within the above LMM (Tables S2 and S3) using packages emmeans and multcomp (Hothorn et al., 2008). Likewise, planned contrasts were used to compare intraploidy versus interploidy competitive effects under different watering treatments (Tables S2 and S3).

To test whether tetraploids are competitively dominant with higher biomass consistently across different watering treatments, we used the LMM with natural log transformed above-ground dry biomass as the response variable as described above (Table S3). The significance of watering treatment indicates that reduced soil water content influenced above-ground biomass, with significantly reduced biomass as the evidence for stress. Planned contrasts within the LMM (Table S3) were used to test whether tetraploids had higher above-ground biomass than diploids under both normal and reduced watering.

To evaluate whether and how tetraploids and diploids differ in functional traits, we conducted LMMs for individual traits separately. In all the LMMs, response variables were power transformed if necessary to improve normality with the optimal power parameter determined using the Box–Cox method in the package car (power parameter = 1, no transformation, for all variables; Fox & Weisberg, 2011). The predictors included ploidy and watering and their interaction (Table S4). The significance of ploidy–watering interaction indicates differences in trait plasticity between diploids and tetraploids. For the random effects, we used the row or column of pots in the functional traits experiment, whichever explained more variation in the LMMs, but not both due to difficulties in achieving model convergence. In the functional traits experiment, we did not include maternal families in the random effects, because maternal families explained less variation than pot positions and often influenced model convergence.

3 | RESULTS

3.1 | Competitive asymmetry under both normal and reduced watering

Consistent with the competitive asymmetry hypothesis (polyploid dominance), the competitive effect of tetraploids on diploids ($\alpha_{2x,4x}$) was stronger than that of diploids on tetraploids ($\alpha_{4x,2x}$; RII

LMM, interploidy density–ploidy interaction, $F=34.5$, $p<0.001$; Figure 3a; Table S2). Specifically, the competitive effect was 1.67-fold higher for tetraploids relative to diploids under normal watering (LS mean \pm SE, $\alpha_{2x,4x} = -0.14 \pm 0.01$, $\alpha_{4x,2x} = -0.09 \pm 0.01$; Figure 3b; Table S2). Reduced watering did not significantly reduce the competitive effect of tetraploids or diploids (normal vs. reduced watering: $\alpha_{2x,4x}$, $t=0.9$, $df=197$, $p=0.35$; $\alpha_{4x,2x}$, $t=-1.3$, $df=173$, $p=0.21$; Figure 3b; Table S2). As a result, the competitive asymmetry of tetraploids versus diploids was maintained under reduced watering ($\alpha_{2x,4x}$ vs. $\alpha_{4x,2x}$, $t=-5.1$, $df=192$, $p<0.001$; Figure 3a,b; Table S2).

Consistent with the expectation that intraploidy effect is stronger than interploidy effect in polyploids (Figure 1b), the magnitude of $\alpha_{4x,4x}$ was 1.6-fold higher than $\alpha_{4x,2x}$ under normal watering (-0.14 ± 0.02 vs. -0.09 ± 0.01 , $z=2.0$, $p=0.049$; Figure 3c; Table S2). This pattern was weakened under reduced watering ($\alpha_{4x,4x} = -0.11 \pm 0.02$ vs. $\alpha_{4x,2x} = -0.07 \pm 0.01$, $z=1.8$, $p=0.077$). For diploids, consistent with the expectation that intraploidy effect is weaker than interploidy effect (Figure 1b), the magnitude of $\alpha_{2x,2x}$ was half of $\alpha_{2x,4x}$ under normal watering (-0.06 ± 0.02 vs. -0.14 ± 0.01 , $z=-3.1$, $p=0.002$), and this pattern held under reduced watering (-0.04 ± 0.02 vs. -0.16 ± 0.01 , $z=-4.7$, $p<0.001$; Figure 3c; Table S2). These results of interploidy and intraploidy competitive effects based on RII (Figure 3; Table S2) were consistent with those based on above-ground biomass (Figure S4; Table S3).

In addition to intraploidy and interploidy competitive effects, the competitive dominance of tetraploids was also reflected by the overall higher above-ground biomass (LMM, ploidy main effect: $F=21.5$, $p<0.001$; Table S3). While tetraploids and diploids experienced a significant reduction in above-ground biomass with reduced watering (watering main effect: $F=4.4$, $p=0.037$), tetraploids maintained higher above-ground biomass over diploids under both normal and reduced watering (normal watering, $\chi^2=223$, $df=1$, $p<0.001$; reduced watering, $\chi^2=262$, $df=1$, $p<0.001$; Figure S4; Table S3). This pattern (with the LMM considering diploid and tetraploid plant

density in a pot simultaneously) was consistent with the case that considered the total density in a pot (regardless of plant ploidy levels; Figure S5).

3.2 | Functional traits explaining the competitive dominance of polyploids

Under normal watering, tetraploids showed more resource-acquisitive traits relative to diploids (Figure 4; Figure S6; Table S4), including higher maximum photosynthesis rate (A_{max} , $\chi^2=18.2$, $df=1$, $p<0.001$), stomatal conductance (g_s , $\chi^2=63.6$, $df=1$, $p<0.001$; Figure S6), transpiration rate (E , $\chi^2=5.0$, $df=1$, $p=0.025$) and TWU ($\chi^2=36.0$, $df=1$, $p<0.001$), as well as lower leaf mass per area (LMA, $\chi^2=11.0$, $df=1$, $p=0.001$). Meanwhile, tetraploids and diploids showed similar WUE (Figure 4), including WUE_i ($\chi^2=0.002$, $df=1$, $p=0.96$), WUE_L ($\chi^2=1.0$, $df=1$, $p=0.31$) and $\delta^{13}C$ that reflects photosynthetic WUE integrated over the life span of a leaf ($\chi^2=1.1$, $df=1$, $p=0.29$). In addition, tetraploids and diploids had similar leaf water potential ($\Psi_{predawn}$, $\chi^2=0.5$, $df=1$, $p=0.47$; Figure 4) and RWC ($\chi^2=0.1$, $df=1$, $p=0.76$; Figure S6).

By contrast, under reduced watering, tetraploids showed more resource-conservative traits relative to diploids (Figure 4; Figure S6), including higher WUE_i ($\chi^2=9.3$, $df=1$, $p=0.002$; WUE_L , $\chi^2=15.4$, $df=1$, $p<0.001$; $\delta^{13}C$, $\chi^2=11.4$, $df=1$, $p=0.001$), lower $\Psi_{predawn}$ ($\chi^2=9.4$, $df=1$, $p=0.002$) and lower RWC ($\chi^2=14.3$, $df=1$, $p<0.001$), while keeping similar levels of gas exchange as diploids (A_{max} , $\chi^2=2.9$, $df=1$, $p=0.09$; g_s , $\chi^2=0.1$, $df=1$, $p=0.75$; E , $\chi^2=2.8$, $df=1$, $p=0.10$). While LMA was lower in tetraploids relative to diploids, LMA increased under reduced watering (4x, $\chi^2=7.4$, $df=1$, $p=0.006$; 2x, $\chi^2=8.8$, $df=1$, $p=0.003$).

As a result, tetraploids exhibited higher trait plasticity than diploids in response to reduced soil water content in water use related traits (WUE_i , WUE_L , $\delta^{13}C$, $\Psi_{predawn}$, and RWC: ploidy–watering

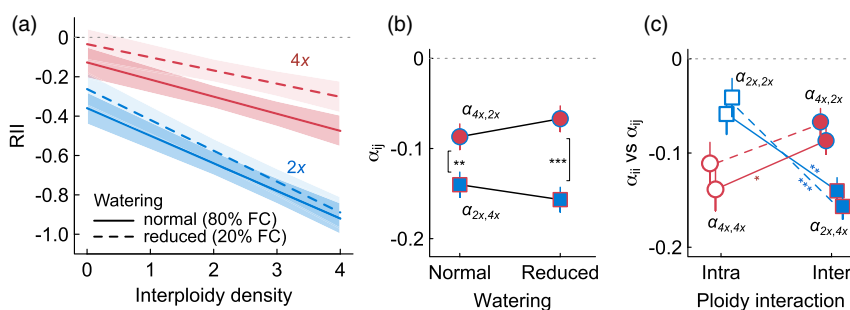


FIGURE 3 Experimental evidence for competitive asymmetry between polyploids and diploids. (a) Competition experienced by tetraploids and diploids (measured using the relative interaction index, RII) intensified as their interploidy competitors increased in density, while controlling for the effects of intraploidy competitor density and other factors as revealed by a general linear mixed model. The interploidy competitive effect (slope, with shaded 95% confidence intervals) was stronger on diploids than tetraploids under both normal watering where soil water content was maintained at 80% field capacity (FC, solid lines) and reduced watering (20% FC, dashed lines). (b) The least-squares mean (LS mean) \pm SE of interploidy competitive effect (α_{ij} , where i and j refer to 2x or 4x, respectively) are plotted. (c) The LS mean \pm SE of intraploidy (α_{ii}) versus interploidy competitive effect (α_{ij}) are plotted. Significant contrasts of LS means are denoted (vertically and along the connecting lines): *** $p<0.001$; ** $p<0.01$; * $p<0.05$. For statistical details, see Table S2.

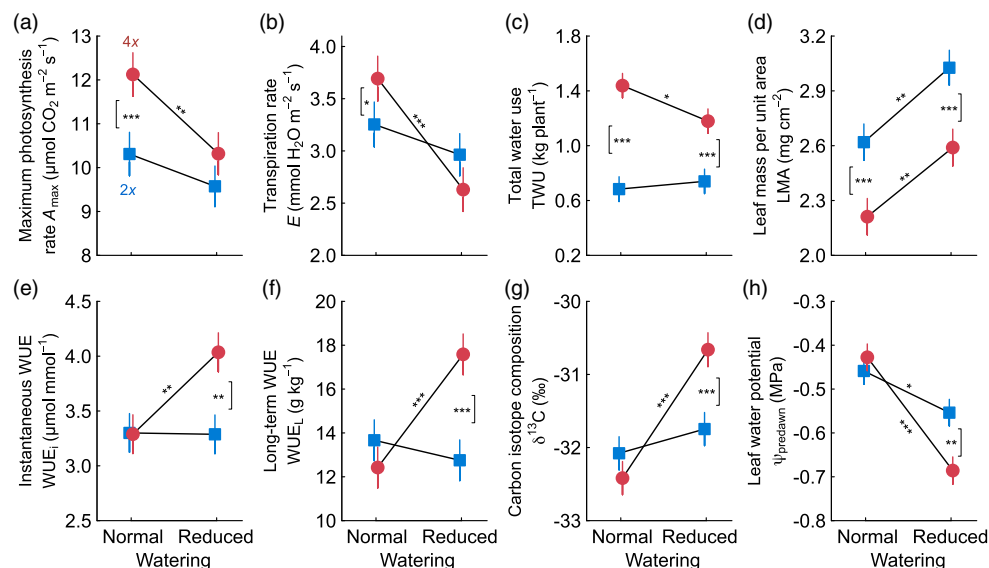


FIGURE 4 Polyploids are more resource acquisitive under normal watering and more drought tolerant under reduced watering than diploids. (a–h) Soil water content was maintained at 80% field capacity (FC) under normal watering and 20% FC under reduced watering. The least-squares mean (LS mean) \pm SE of individual functional traits (Table 1) are plotted for diploids (blue squares) and tetraploids (red circles), estimated from general linear mixed models. WUE, water use efficiency. Significant contrasts of LS means are denoted (vertically and along the connecting lines): *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. For statistical details, see Table S4.

interaction, all $p < 0.05$; Table S4), as well as stomatal conductance and transpiration rate (Table S4), while trait plasticity was similar between the two ploidy levels in A_{max} , TWU and LMA.

4 | DISCUSSION

By quantifying the intensity of interploidy and intraploidy competitions, our results provided strong evidence for the competitive asymmetry between polyploid and diploid plants in *C. indicum*, with tetraploids that are geographically more widespread being competitively dominant to diploids. As a stronger competitor, tetraploids were limited more strongly by individuals of their own than by diploid individuals, and the predicted reverse pattern was detected in diploids. Such competitive asymmetry was not only maintained under reduced soil water content, but also translated into higher fitness component (above-ground biomass) of tetraploids than diploids consistently across different soil water conditions. Our results further revealed that functional traits associated with fast growth and efficient water use may explain the competitive dominance of tetraploid *C. indicum*.

4.1 | Polyploids are competitively dominant relative to diploids

Our results support the hypothesis that competition between polyploids and diploids is asymmetric in *C. indicum*. The competitive abilities of polyploids and diploids have often been evaluated by two different methods: 'direct' assessment that informs the strength of

competitive effect that one ploidy may exert on another when encountering each other (polyploid–diploid competition) (e.g. Maceira et al., 1993; Rey et al., 2017; Thompson et al., 2015; this study) and 'indirect' assessment that considers the possibility that co-occurring polyploids and diploids may have other more immediate competing neighbours (polyploid–other species vs. diploid–other species competition) (Čertner et al., 2019). Similar to our findings, previous studies using direct assessments have revealed stronger competitive effects of polyploids compared to diploids, such as in allotetraploid forb *Centaurea stoebe* (Collins et al., 2011) and autotetraploid grass *Dactylis glomerata* (Maceira et al., 1993) under benign conditions. Likewise, indirect assessments have revealed lower fitness loss of polyploids than diploids when competing with other plant species, such as in herbaceous autotetraploid *Knautia serpentinicola* (Čertner et al., 2019), autotetraploid *Lolium perenne* (Sugiyama, 1998), and autotetraploid and autohexaploid *Solidago canadensis* (Cheng et al., 2020). These previous studies and ours provide empirical evidence for the dominance of polyploids over diploids across various approaches, types of polyploidy (including auto- and allopolyploidy) and polyploid complex systems.

Also consistent with the predictions (Figure 1; Figures S1 and S2), the competitively dominant tetraploid *C. indicum* experienced stronger intraploidy than interploidy competition especially under normal watering (80% FC) in this study. This pattern was seen previously in autotetraploid perennial grass *D. glomerata* (Maceira et al., 1993) where intraploidy competitive effect was stronger than interploidy effect ($\alpha_{4x,4x} > \alpha_{4x,2x}$), and the predicted reverse pattern of weaker intraploidy than interploidy competition ($\alpha_{2x,2x} < \alpha_{2x,4x}$) was observed in its diploid plants. In allotetraploid annual grass *Brachypodium hybridum* (Rey et al., 2017), $\alpha_{4x,4x} > \alpha_{4x,2x}$

was also detected; but the prediction of $\alpha_{2x,2x} < \alpha_{2x,4x}$ in its diploid plants (*B. distachyon*) was environment dependent and was only observed in drier environments. Different from these findings, in perennial forb *Chamerion angustifolium* (Thompson et al., 2015), similar levels of intraploidy and interploidy competition effects were observed in both the autotetraploid and diploid plants. These differences in empirical support for intra- versus interploidy competition indicate the complexity of species interaction and its context dependence, which can vary with other factors, for instance, different evolutionary histories of distinct polyploid lineages and local adaptation of polyploid and diploid populations to their home environments that can be different from experimental conditions (Rosche et al., 2018; Wei et al., 2020). Thus, additional research is needed for a more complete understanding of species interactions between and within ploidy levels across diverse polyploid complex systems and environments.

4.2 | Competitive asymmetry is maintained under reduced soil water content

Our results did not provide strong evidence for the SGH that predicts weakened competitive interactions with increased resource stress. While reduced soil water content (from 80% to 20% FC) imposed stress on the tetraploid and diploid plants as evidenced by significantly reduced above-ground biomass, the lack of significant differences in competitive effect ($\alpha_{2x,4x}$, $\alpha_{4x,2x}$, $\alpha_{4x,4x}$, $\alpha_{2x,2x}$) between the two soil water conditions likely have several reasons. First, at 20% FC where water was extremely limited, plants may show strong competition for this essential resource, whereas at 80% FC where water was less limited, plants may compete for other essential resources (e.g. light, nutrition, limited space in the fixed-size pots) and thus exhibiting strong competition at both conditions. Second, competition measured in this study focused on one important fitness component, vegetative growth, in perennial *C. indicum*. While vegetative robustness in perennial plants especially those capable of clonal reproduction likely positively affects sexual reproduction and overall fitness (Aschehoug et al., 2016; Cheplick, 2020; Fujita et al., 2014; Wei et al., 2019), it remains to be evaluated how competition based on other fitness measures (e.g. sexual reproduction) in perennial *C. indicum* change with increased resource stress, and whether it will follow the prediction of SGH as seen in annual grass *Brachypodium* (Rey et al., 2017). In *Brachypodium*, the interploidy competitive effects of diploid *B. distachyon* and allotetraploid *B. hybridum* measured based on seed production decreased in drier conditions (Rey et al., 2017), in line with SGH. Third, the resource stress level and how plants cope with the imposed resource stress can also influence the outcome of species interactions. As *C. indicum* especially the tetraploids often occur in dry habitats (Li et al., 2014), they likely have evolved strategies to cope with severe water stress in the wild, which might be more severe than a constant soil water content at 20% FC here, and thus they may still exhibit strong competition with diploids.

Overall, as factors including stress types, fitness measures, other limiting factors and characteristics of interacting species can influence the strength of species interactions along stress gradients (He et al., 2013), it is important to consider these factors when evaluating SGH in polyploid complex systems.

The competitive asymmetry between tetraploid and diploid *C. indicum* was maintained under reduced soil water content. While competitive asymmetry was found to vary with environments between diploid *B. distachyon* and allotetraploid *B. hybridum* (Rey et al., 2017), the maintenance of competitive asymmetry in *C. indicum* under both low and high soil water contents translated into higher above-ground biomass of tetraploids than diploids. Such fitness strategy may result from changes in functional traits and trait plasticity owing to increased genomic redundancy and expression versatility following polyploidy and may underlie the range expansion of tetraploid *C. indicum* and habitat displacement of its diploid counterpart during the geological period of drought in the Quaternary (Li et al., 2014).

4.3 | Functional traits explain the competitive dominance of tetraploid *C. indicum*

Tetraploid *C. indicum* expressed traits that can confer faster growth under high soil water content (80% FC) and more efficient water use under reduced soil water content (20% FC) compared to diploid *C. indicum*, which may underlie the competitive dominance of tetraploids. Under high soil water content (80% FC), the acquisitive strategy of tetraploids was manifested by higher gas exchange (A_{\max} , g_s , E) and higher TWU. The higher rates of gas exchange could contribute to the stronger growth performance of tetraploids than diploids in *C. indicum*, which has also been observed in other polyploid complex systems (Liao et al., 2016; Vyas et al., 2007). In *C. indicum*, tetraploids had lower LMA (higher SLA), which may contribute to greater photosynthetic capacity and higher biomass accumulation (Reich et al., 1997; Westoby et al., 2002). Although LMA is often thought to be higher in polyploids relative to diploids (e.g. Greer et al., 2018; Li et al., 2009; Wei et al., 2019, 2020), the reverse pattern as observed in *C. indicum* has also been reported in other plants such as grass *Brachypodium* (Manzaneda et al., 2015). The lack of consistency in LMA patterns between polyploids and diploids may be explained by its weak relationship with genome size (Knight & Beaulieu, 2008). Under reduced soil water content, tetraploids exhibited higher WUE, which may benefit tetraploids in conserving water for growth under water deficiency (Greer et al., 2018; Manzaneda et al., 2015). In addition, tetraploids were able to maintain gas exchange at a similar level as diploids but at lower leaf water potential (Ψ_{predawn}) and leaf RWC, indicating stronger drought tolerance of tetraploids. Different from drought tolerance in tetraploid *C. indicum*, drought avoidance was found in autotetraploids in *Lonicera japonica* (Li et al., 2009), *Chamerion angustifolium* (Maherali et al., 2009) and *Citrus sinensis* (Oliveira et al., 2017), where autotetraploids exhibited higher Ψ_{predawn} and RWC under drought. The shift of ecological strategies from resource acquisitive to resource

conservative in tetraploid *C. indicum* with reduced soil water content suggests that polyploidy may play a vital role in promoting trait plasticity and adaptive responses to changing environments (te Beest et al., 2012; Wei et al., 2019).

To conclude, our study provides a quantitative demonstration of the competitive asymmetry between polyploids and diploids consistently across different soil water conditions. This offers an important mechanistic insight into the ecological advantage of polyploids (Van de Peer et al., 2021; Wei et al., 2019) and the underlying functional traits. Our study focused on established polyploids and diploids; as such, the competitive dominance of tetraploid *C. indicum* may reflect the combined effects of polyploid formation and polyploidy-enabled adaptation. This finding awaits similar tests in natural or synthetic neopolyploids, whose phenotype and fitness can be quite dynamic during the initial stages of polyploid formation. We should note that our study quantified interploidy and intraploidy competitions based on individual-level performance (biomass) rather than population-level performance (e.g. per capita growth rate) due to the perenniality of this polyploid complex and short-term stress experiment under a substantial reduction in soil water content. Future work based on population-level performance (Adler et al., 2018; Aschehoug et al., 2016; Hart et al., 2018) is needed from both annual and perennial polyploid complex systems (over multiple years) to shed lights on the conditions of competitive exclusion or coexistence between polyploid and diploid plants across heterogeneous environments. Together, these studies will yield important insights into the roles of competition and habitat filtering in driving the distribution of polyploid and diploid plants in the face of environmental change.

AUTHOR CONTRIBUTIONS

Wen Guo, Yuan-Wen Duan and Yong-Ping Yang designed the research and Na Wei conceived the conceptual development of the manuscript. Wen Guo conducted the glasshouse experiments. Na Wei conducted data analyses and visualization. Wen Guo and Na Wei wrote the manuscript, and all authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

All authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.7m0cfxq08> (Guo et al., 2023).

ORCID

Wen Guo  <https://orcid.org/0000-0003-4166-5140>

Na Wei  <https://orcid.org/0000-0002-7345-501X>

Guang-You Hao  <https://orcid.org/0000-0002-6003-7003>

Shi-Jian Yang  <https://orcid.org/0000-0002-1430-3251>

Zhi-Yong Zhu  <https://orcid.org/0009-0009-7671-7490>

Yong-Ping Yang  <https://orcid.org/0000-0002-0327-2664>

Yuan-Wen Duan  <https://orcid.org/0000-0002-8399-5116>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

- Figure S1.** Hypotheses of interploidy competition in response to stress.
- Figure S2.** Hypotheses of intraploidy versus interploidy competition in response to stress.
- Figure S3.** Competition experiment design.
- Figure S4.** Experimental evidence for competitive asymmetry between tetraploids and diploids based on above-ground biomass.

Figure S5. Competition experienced by tetraploids and diploids intensified as total plant density increased.

Figure S6. Stomatal conductance and leaf relative water content of tetraploids and diploids.

Table S1. Sampling information of diploid and tetraploid *Chrysanthemum indicum*.

Table S2. General linear mixed model and planned contrasts examining competitive interactions.

Table S3. General linear mixed model and planned contrasts examining above-ground biomass.

Table S4. General linear mixed models and planned contrasts examining functional traits.

Appendix S1. Functional traits experiment.

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