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Research Article

Friends or foes? Polyploidy and competition in a grassland geophyte

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Previous studies have suggested polyploids may possess a competitive advantage over diploids, due to their larger size, increased vigour or ability to better respond to abiotic stress. However, few studies have tested the effect of polyploidy on competitive ability directly, and only relatively recently has this oversight begun to be addressed. Here we assessed potential differences in competitive ability between diploids and tetraploids of a widespread African grassland geophyte, *Oxalis obliquifolia*. Diploid and tetraploid plants were grown in identical environmental conditions under four different competition scenarios. As a control, diploids and tetraploids were grown under solitary conditions. For intra-cytotype competition, pairs of diploids and tetraploids were planted together. Inter-cytotype competition involved planting individual diploids and tetraploids with one another, and for interspecies competition individual diploids and tetraploids were planted with *Themeda triandra* seedlings. Thirty-seven morphological, physiological and phenological traits were recorded and assessed for associations between cytotype and competition treatment using ordinations and GLMs. Ordination showed diploids and tetraploids as distinct clusters, with very little separation based on competition treatment. Univariate analyses showed tetraploids have larger but fewer organ structures than diploids, suggesting a tradeoff between these traits. Tetraploids also produce larger seeds. Diploids showed reduced numbers of leaves and were more negatively impacted by interspecies competition than tetraploids, suggesting tetraploids may potentially be the better interspecies competitor. Tetraploids also extended their flowering season in response to inter-cytotype and interspecies competition. Cytotypes respond differently under different competition treatments, and tetraploids may have a competitive advantage over diploids. However, this potential competitive asymmetry does not explain observed cytotype sympatry. Tetraploids also appear to differentiate between intra-cytotype competition, and competition with diploids and other species. The potential for abiotic factors to impact these competition dynamics remains unexplored.

Key words: competition, geophyte, polyploidy, sympatry

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Introduction

Whole-genome duplication (WGD), or polyploidy, is a well-documented genome-level mutation that is especially prevalent amongst the angiosperms (Wood et al. 2009, Jiao et al. 2014). Many extant diploid seed plants and angiosperms are thought to be descended from ancient polyploids (Soltis et al. 2009), and the prevalence of polyploidy as a major force in plant evolution is further demonstrated by its continued persistence among many species' populations across the world (Rice et al. 2019). Patterns of cytogeography can vary greatly from region to region, ranging from polyploid sympatry (for example in Vaz de Sousa et al. 2024), parapatry (Castro et al. 2020), and allopatry (Peirson et al. 2012), and can be shaped in part by differences in traits associated with polyploidy. Due to polyploidisation events often resulting in immediate consequences for plant physiology, it can have potentially important repercussions for plant ecology, and in particular plant competitive ability (Anneberg et al. 2023).

Newly formed polyploids emerge into the context of an existing diploid population. Theoretical models have suggested that initial minority cytotype disadvantage (Levin 1975, Chrtek et al. 2017) ought to make polyploid establishment and persistence very unlikely (Levin 2002, Ramsey and Schemske 2002), and that most nascent polyploids are more likely to go extinct (Levin 1975, Husband 2000) due to competitive exclusion by their locally adapted, and more abundant, diploid parents (Fowler and Levin 1984, 2016, Husband 2000, Arrigo and Barker 2012). Faced with such a challenge, successful polyploid establishment would be dependent on either avoiding competition with diploids via ecological niche differentiation, or by successfully outcompeting their diploid parents (Fowler and Levin 1984, 2016, Rodríguez 1996). Both abiotic niche differentiation and asymmetrical competitive ability among cytotypes would ultimately result in segregated spatial distribution patterns, however, there are a few instances where cytotypes are known to occur in sympatry with one another across the study area (for example, Husband and Schemske 2000, Sonnleitner et al. 2015, Vaz de Sousa et al. 2024), and they often cooccur in contact zones between otherwise distinct distributions (as in Eliášová and Münzbergová 2017, Wefferling et al. 2017, Muñoz-Pajares et al. 2018, Duchoslav et al. 2020).

Polyploidisation can result in immediate changes to plant phenotype (Ramsey and Schemske 2002, Clo and Kolář 2021), potentially altering plant morphological (Corneillie et al. 2019, Bomblies 2020), ecophysiological (Ramsey and Ramsey 2014) and/or phenological traits (Levin 2002). Changes to plant phenotype can in turn manifest changes in plant growth and response to both abiotic and biotic factors (McArthur and Sanderson 1999, Maherali et al. 2009, Castro et al. 2023). Additionally, polyploids may display greater adaptability and tolerance to abiotic stresses and fluctuations than diploids (McIntyre 2012, Allario et al. 2013, Van de Peer et al. 2021), which has also been linked to the ability of polyploids to expand their range (Treier et al. 2009, te Beest et al. 2012) and may also impact polyploid competitive ability.

The Gigas effect, referring to the overall increase in cell and organ size due to polyploidy, is one well documented instance of change to plant physical traits at the individual level (Müntzing 1936, Stebbins 1971, Masterson 1994, Otto 2007). This increased size of the polyploid individual has been viewed as potentially adaptive, in the context of competition between polyploids and their smaller diploid parents (Stebbins 1971, Levin 2002, Ramsey and Schemske 2002), but this has rarely been tested directly. Putative competitive advantages include the increased size, with polyploids producing larger flowers and seeds (Garbutt and Bazzaz 1983, Levin 1983, Bretagnolle et al. 1995, Segraves and Thompson 1999), but also increased vigour compared to diploids and potentially greater seedling vigour (Blossey and Nötzold 1995, Jakobs et al. 2004, te Beest et al. 2012, Van de Peer 2021). However, polyploidisation can also result in potential disadvantages, such as problems linked to chromosome pairing and segregation during meiosis and mitosis (Comai 2005), as well as challenges to efficient cell functioning due to increased cell size and changes to cell surface area to volume ratios (a condition that may have substantial consequences for plant physiological processes, such as changes to rates of photosynthesis, gaseous exchange and transpiration; Levin 2002, Comai 2005), and potentially slower plant growth rates (Ramsey and Schemske 2002).

Competitive interactions among cytotypes can be highly complex (Guo et al. 2023, Rodríguez-Parra et al. 2025). In circumstances where polyploids are better interspecific competitors than diploids, it could result in range expansion of the polyploid individuals beyond the range of their diploid parents (Maceira et al. 1993, Manzaneda et al. 2012), assuming that biotic factors are the main limiting factors to distribution and without accounting for other abiotic factors and dispersal constraints that may also affect range. Additionally, polyploids may display increased inter-cytotype competitive ability, meaning that they may display competitive dominance over their diploid counterparts (Maceira et al. 1993, Guo et al. 2023). Under such circumstances it is expected that the polyploids would displace diploids, and so a population would change from one of initially mixed cytotypes, to having a single dominant higher ploidy cytotype (Maceira et al. 1993, Buggs and Pannell 2007).

Consideration must also be given to the role of intracytotype competition (Castro et al. 2023) and the effects it may have on patterns of cytogeography. The performance of polyploids when competing against one another, relative to their performance when competing against diploids, may also impact the distribution of cytotypes. Similar to interacting species, we can view competitive dynamics of interacting cytotytpes according to the Lotka–Volterra model of competition, which in turn contributed to the rise of the competitive exclusion principle, first proposed by Gause in 1934 (Godsoe et al. 2015, Gavina et al. 2018). It is possible that sympatry may be favoured in situations where the negative effects on cytotype (diploid or polyploid) performance caused by intra-cytotype competition is larger than the negative effects caused by inter-cytotype competition. In other words, both cytotypes, although still competing with one another, perform better when competing against each other, than with individuals of the same ploidy.

Previously these effects have often been tested indirectly, by measuring traits like above-ground and/or below-ground biomass accumulation, differences in whole plant, plant organ and cell size, as well as functional trait differences, between diploid and polyploid plants that are grown separately (Anneberg et al. 2023). Often differences in one or more of these traits in polyploid individuals, that may or may not be beneficial in a particular context, will involve tradeoffs with other traits that also may impact plant survival and response to environmental factors (Thébault et al. 2011, Leitch and Leitch 2022). Additionally, these effects may change substantially when diploids and polyploids are grown in direct competition with one another. Although the impacts of interspecific and intraspecific (or in the case of this study, intra-cytotype and inter-cytotype) competition involving polyploids and diploids are likely to be important factors in the ecology and cytogeography of polyploid complexes, there are only a limited number of studies that have explored this topic in-depth (Maceira et al. 1993, Collins et al. 2011, Thompson et al. 2015, Rey et al. 2017, Čertner et al. 2019, Castro et al. 2023, Guo et al. 2023). Furthermore, it is notable that all these studies are focused on polyploid complexes in the global north. Almost nothing is known about polyploid competition dynamics from populations in the southern hemisphere generally, and from African geophytic species more specifically. Differences in competitive ability among cytotypes may help to explain observed patterns in local species cytogeography.

In this study we set out to assess the effects of polyploidy on plant competitive ability under different competition scenarios, using a grassland geophyte from southern Africa as the model organism, and to explore various hypotheses relating to their possible competition dynamics. First, we tested if competition would impact plant performance (for both diploids and tetraploids), by comparing plants grown under solitary conditions to plants grown alongside others of the same cytotype (intra-cytotype competition). Secondly, given that we observe cytotype sympatry in wild populations, and given the principles outlined by the Lotka–Volterra model of competition dynamics that would favour sympatric distributions, we hypothesised that plants would be more negatively impacted by intra-cytotype competition effects than by inter-cytotype competition effects (as measured via a suite of plant functional and performance traits). Finally, we tested whether differences in interspecies competitive ability exist between diploids and tetraploids, as determined by differences in plant functional and performance traits. These effects were assessed using measured morphological, phenological and physiological traits, as reliable predictors of cytotype, when plants are grown under distinct competition treatments, specifically solitary, intra-cytotype, inter-cytotype, and interspecies competition conditions.

Material and methods

Study species

Oxalis obliquifolia (Oxalidaceae) is a bulbous perennial with the largest distribution range of all African *Oxalis* species, from the eastern, summer-rainfall regions of South Africa (Exell 1963) north to Ethiopia (Raimondo et al. 2009), Eritrea (Edwards et al. 2000) and Sudan (Darbyshire et al. 2015). Seasonal leaves are borne on an emergent rhizome with inflorescences developing from the leaf axils. Tristylous flowers occur solitarily on peduncles that tend to be longer than the surrounding leaves. The species flowers during the rainy months of the austral summer (during the months of October to February, Vaz de Sousa et al. 2024). Clonal offspring are the result of bulbils produced vegetatively from the parent bulb, or from the subterranean rhizome.

Although only a relatively small portion of its overall distribution has been assessed, *O. obliquifolia* possesses impressive cytotype diversity (Vaz de Sousa et al. 2024), including diploids, tetraploids, pentaploids, hexaploids and octoploids. The age of the polyploid lineages, as well as the mode of polyploidisation (auto- versus allo-) is unknown, although the facts that diploids and polyploids are morphologically indistinguishable in the field, and that no close relatives co-occur over much of the species' range, suggests autopolyploidy. Interestingly, and of relevance here, different cytotypes are often sympatric. A distinct Gigas effect is present across both somatic and reproductive organs when grown individually (Vaz de Sousa et al. 2024). Diploids and polyploids seem to share the same abiotic niche, but have substantially reduced inter-cytotype seed set, and are effectively reproductively isolated from one another in the wild. Although abiotic niche separation (Vaz de Sousa et al. 2024) and pollinator-driven competition (Vaz de Sousa unpubl.) between cytotypes have been assessed as possible causes of this unusual inter-cytotype sympatry, the role of direct competition (or lack thereof) between plants in this species has not received attention.

Competition experiment

A total of 110 individuals (56 diploids, 54 tetraploids), roughly equally gathered (subject to bulb availability) from 16 different populations were available from a previous study (Vaz de Sousa et al. 2024) and were used in this competition experiment. In order to test possible competition dynamics, four distinct competition treatments were defined for this trial, including solitary individuals (22 replicates, 12 diploids and 10 tetraploids) as a control group, intra-cytotype competition (20 replicates, 20 diploids and 20 tetraploids), inter-cytotype competition (20 replicates, 10 diploids and 10 tetraploids) and interspecies competition (22 replicates, 11 diploids and 11 tetraploids). For intra-cytotype competition, either a pair of diploid or a pair of polyploid bulbs were planted together in the same pot. For inter-cytotype competition, a diploid and a polyploid bulb were planted together. Interspecies competition included individual diploids and polyploids that were planted with a locally occurring grass species *Themeda triandra* (seeds acquired from Silverhill Seeds nursery, South Africa). Initial bulb size effects were controlled for by size matching bulb pairs. All bulbs were planted at a depth of 5 cm below the surface in 15 × 15 cm plastic pots containing a homogenised mixture of sand and potting soil. Individual plants were planted 5 cm apart for pots containing two plants. Bulbs were allowed to acclimate and enter dormancy for a full season (from May 2023 to mid-August 2023) prior to the beginning of the trial. For the interspecies treatment, 2-week-old *T. triandra* seedlings of equal size (about 6 cm tall) were planted 3 days prior to initial watering.

Plants were grown under controlled and uniform environmental conditions. To encourage breaking of bulb dormancy, plants were initially watered (on 15 August 2023) two weeks prior to placing them into a growth chamber (Conviron PGC FLEX - 2 Tier, Controlled Environments Limited) for a total of 192 days (1 September 2023–10 March 2024). Carbondioxide concentrations were maintained at approximately 400 ppm, and relative humidity (RH) at 40%, to simulate local ambient conditions (Franklin 1998). Maximum light intensity was set between 350 and 400 PAR (μmol m^{-2} s^{-1}). Photoperiod length (day/night hours) were adjusted on a monthly basis, to reflect mid-monthly averages for Gauteng Province, South Africa (www.timeanddate.com/sun/@1105782?month=3&year=2024, see the Supporting information). Average maximum day and minimum night temperatures (°C), as well as mean precipitation (imitated by controlled irrigation; mm day^{-1}) were set to simulate monthly baseline conditions (Supporting information) as described in the International Panel on Climate Change, Sixth Assessment Report (AR6) for the east southern African region (IPCC 2022, 2023). Plants were randomly shuffled once a week to minimise the effect of possible systematic micro-climate variation.

Crossing experiment

In order to test for potential differences in seed size, diploid and tetraploid seeds (340 and 301 seeds respectively) were obtained from a previous pollination experiment (Vaz de Sousa et al. 2024). Dormant seeds were stored under dry, cool (not higher than 20°C), and dark conditions for no longer than 18 months, prior to weighing. Pollination treatments included legitimate intra-cytotype crosses with both diploid (38 successful crosses) and tetraploid (43 successful crosses) parents.

Data collection

A total of 37 plant traits were selected (including morphological, phenological and physiological traits relating to plant resource utilisation and general plant performance; see the Supporting information), with the aim of maximising plant trait dimensionality as discussed by Laughlin (2014), together with pre-selected study-specific traits (Supporting information). These traits included plant performance traits (including plant/bulb survival and biomass accumulation, vegetative propagation, photosynthetic rate, intercellular versus ambient CO_2 and water use efficiency) and functional traits (such as foliar and floral size-related traits, organ number traits, plant height, seed mass, plant growing and flowering phenology). Each plant was inspected, and phenological events recorded, every second day for the full duration of the trial. All phenological data were measured as the number of days since initial watering.

Foliar and floral morphological traits, for those plants that survived and emerged, were measured at the peak of the growing season (mid-January 2024). Size measurements were collected with the aid of calipers and a ruler, recorded to an accuracy of 0.5 mm. Foliar traits were recorded using the largest mature leaf available per plant on any given data collection day. Floral traits were recorded from the first flower to open after the assigned measurement date and when flowers were fully open. The shape of principle foliar and floral organs was recorded as ratios between size measurements. Bulbs from each plant were collected at the end of the trial (after above-ground senescence) and then counted and weighed individually, and their mass (g) was recorded. Individual seed mass (g) was measured as the response variable for the crossing experiment.

Physiological traits, for those plants that emerged, were measured using a LI-6400XT open path photosynthesis system (Li-Cor), using the following chamber conditions: CO_2 concentration maintained at 400 μmol mol^{-1}; flow rate set to 400 μmol s^{-1}; photosynthetically active radiation (PAR) inside the chamber was maintained between 1500–2000 μmol m^{-2} s^{-1} (LI-6400 XT LED light source); and relative humidity was maintained above 50%. Measurements were recorded as soon as A_n stabilised, which typically occurred within two minutes of the leaf being placed in the chamber. Measurements were taken using only mature leaves and conducted under identical environmental conditions. Recorded traits included photosynthesis/CO_2 assimilation rate (A; μmol m^{-2} s^{-1}), stomatal conductance (g_s; mol m^{-2} s^{-1}) and intercellular CO_2 concentrations (C_i; μmol CO_2 mol^{-1} air) and ambient CO_2 (C_a; μmol CO_2 mol^{-1} air). These measurements were then used to calculate the intrinsic water use efficiency (A/g_s) and the ratio of intercellular CO_2 concentrations to ambient CO_2 (C_i/C_a).

Statistical analyses

Unless otherwise indicated, all statistical analyses were performed in the R statistical environment (Supporting information; ver. 4.2.0; www.r-project.org). Pairwise Pearson's correlations (www.r-project.org) was calculated for morphological and phenological variables to assess for collinearity, and a single variable from any correlated pair with an $|r|$ value of more than 0.7 was randomly selected and retained for analysis (Supporting information). For both univariate and multivariate analyses only surviving bulbs were included, and there was no significant difference in bulb die off between competition treatments with an average of three bulbs lost per treatment class.

A principal component analysis (PCA; Venables and Ripley 2002) was used to visualise multivariate differences in measured morphological and physiological traits (i.e. excluding phenological traits) between different cytotypes using the package 'FactoMineR' (Lê et al. 2008). Statistical support for associations of morphological and physiological traits with both cytotype and competition treatments were then determined using Gower's distance (Gower 1971) and a PERMANOVA using the 'vegan' package (Oksanen et al. 2022), and pairwise comparisons of clusters performed using the package 'pairwise.Adonis' (Martinez 2020). Following this, univariate analyses testing morphological, phenological and physiological differences between cytotypes and competition treatments were conducted using the *glm()* function with the 'stats' package in base R (GLM; www.r-project.org). Data normality for continuous variables was assessed using a Shapiro–Wilk test (Royston 1982) with subsequent Box–Cox tests using the boxcox function (Box and Cox 1964, Venables and Ripley 2002) to estimate values of lambda for best-fit transformations. The fit of each combination of model and data transformation were assessed by comparing Q–Q plots of residuals, AIC values, and residual deviance values. Negative-binomial distributions were used for count data. Post hoc tests were performed using the 'emmeans' package and *emmeans* function for all pairwise comparisons (Lenth 2024). All univariate p-values were adjusted using Benjamini and Hochberg (1995) correction for multiple comparisons (www.r-project.org). See the Supporting information for additional trait response graphs.

Results

Multivariate results

Total explanatory power of the PCA (Fig. 1) for the first two principal components was moderate, accounting for a cumulative 47.80% of the total variation in the data. This cumulative explanatory power increased to 56.64% and 64.00% by the third and fourth principal components, respectively. Diploids and tetraploids were separated in the first two principal components; however, there is very little separation of clusters based on competition treatment (Fig. 1C). Both patterns are confirmed by the PERMANOVA results (Table 1), which shows significant differences between diploid and tetraploid clusters generally, and shows some evidence of significant differences between diploids grown under interspecies competition and diploids grown under solitary or intra-cytotype competition. It is notable that plant performance traits relating to size, for example 'Middle leaflet length', were the largest contributors to the construction of principal component one (Fig. 1A), and that count/number of organ traits, such as 'Number of leaves', was most important in the construction of principal component two.

Morphological traits

In general, the effect of cytotype was far more prominent than competition treatment, however there is some evidence

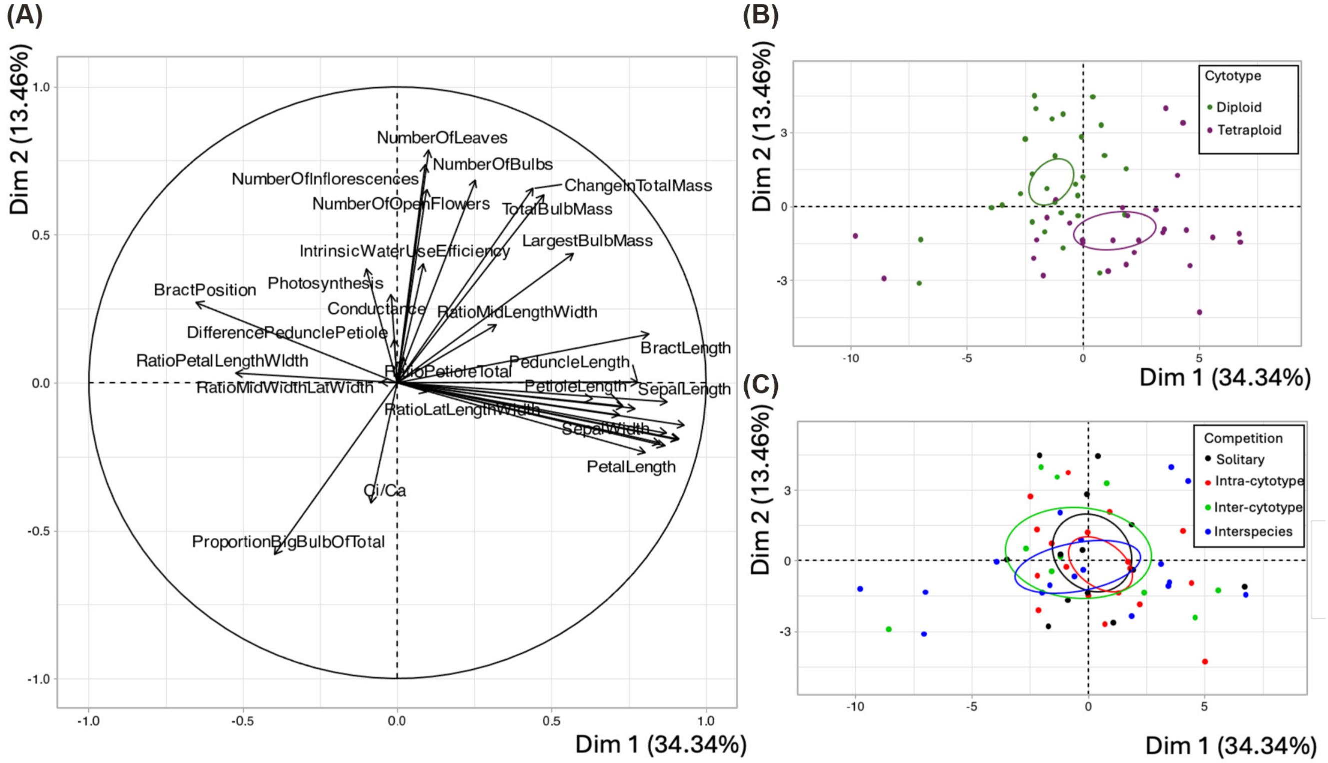

Figure 1. Principal component analysis (PCA) constructed (A) using all 33 quantitative morphological and physiological traits as predictors of (B) cytotype (diploid – green, tetraploid – purple) and (C) competition type (solitary – black, intra-cytotype – red, inter-cytotype – green, interspecies – blue), indicating separation of diploid and tetraploid clusters, but no clear separation based on competition treatment. The 95% confidence ellipses are indicated for each group.

Table 1. PERMANOVA results of plant morphological and physiological traits as predictors of cytotype and/or competition treatment, and post hoc pairwise comparisons of principal component analysis clusters and associated adjusted p-values. * indicates significant p-values.

						Pairwise comparisons of clusters	
	df	Sum of Squares	R^2	F statistic	p-value	Cluster pairs	Adjusted p-value
Cytotype	1	0.26872	0.14584	9.8726	0.001*	Diploid solitary vs Diploid intra-cytotype	0.224
Competition	3	0.08792	0.04771	1.0767	0.370	Diploid solitary vs Tetraploid solitary	0.001*
Cytotype: Competition	3	0.12504	0.06786	1.5313	0.093	Tetraploid solitary vs Diploid intra-cytotype	0.007*
Residual	50	1.36093	0.73859			Diploid solitary vs Diploid interspecies	0.038*
Total	57	1.84260	1.00000			Diploid intra-cytotype vs Diploid interspecies	0.028*
						Diploid interspecies vs Tetraploid solitary	0.026*
						Diploid solitary vs Tetraploid inter-cytotype	0.025*
						Diploid intra-cytotype vs Tetraploid inter-cytotype	0.038*
						Tetraploid solitary vs Tetraploid inter-cytotype	0.626
						Diploid interspecies vs Tetraploid inter-cytotype	0.227
						Diploid solitary vs Tetraploid intra-cytotype	0.002*
						Diploid intra-cytotype vs Tetraploid intra-cytotype	0.001*
						Tetraploid solitary vs Tetraploid intra-cytotype	0.491
						Diploid interspecies vs Tetraploid intra-cytotype	0.004*
						Tetraploid intra-cytotype vs Tetraploid inter-cytotype	0.454
						Diploid solitary vs Tetraploid interspecies	0.015*
						Diploid intrac-cytotype vs Tetraploid interspecies	0.009*
						Tetraploid solitary vs Tetraploid interspecies	0.505
						Diploid interspecies vs Tetraploid interspecies	0.017*
						Tetraploid inter-cytotype vs Tetraploid interspecies	0.37
						Tetraploid intra-cytotype vs Tetraploid interspecies	0.813
						Diploid solitary vs Diploid inter-cytotype	0.491
						Diploid intra-cytotype vs Diploid inter-cytotype	0.571
						Diploid inter-cytotype vs Tetraploid solitary	0.006*
						Diploid inter-cytotype vs Diploid interspecies	0.099
						Diploid inter-cytotype vs Tetraploid inter-cytotype	0.044*
						Diploid inter-cytotype vs Tetraploid intra-cytotype	0.001*
						Diploid inter-cytotype vs Tetraploid interspecies	0.005*

that both plant performance (biomass accumulation) and functional traits (organ number and flowering phenology) responded differently to different types of competition. Beginning with the above-ground traits, significant differences between cytotypes were observed across three uncorrelated, size-related morphological traits (Middle leaflet length, Petal width and Peduncle length), with polyploids consistently larger than diploids under all competition treatments (Table 2, Fig. 2A). These size differences were also consistent across all correlated, size related traits. Only one shape-related trait (Ratio of flower diameter to petal length) differed consistently between diploids and polyploids, where polyploids had broader flowers than diploids. Importantly, there were no significant differences observed between solitary and intra-cytotype competition treatments for all traits assessed (Table 2, Fig. 2). Furthermore, intra-cytotype and inter-cytotype competitive effects only differed for a single trait (Number of bulbs produced after one growing season), suggesting very limited differences in the effects between these two competition treatments on overall plant performance.

Traits related to number of organ structures (Number of leaves, Number of inflorescences and Number of bulbs produced after one growing season) showed more complex patterns, with significant interactions between cytotype and competition treatment (Table 2, Fig. 2). Diploids tended to produce higher numbers of leaves (Fig. 2B) and inflorescences (Fig. 2C) than tetraploids under all competition scenarios except interspecies competition, where they displayed a reduction in the number of leaves and flowers they produced. For leaves this reduction was so large that the difference between diploids and tetraploids disappeared entirely. The pattern for inflorescences under inter-species competition was similar but not significantly different between cytotypes (Fig. 2C).

With regards to below-ground traits, diploids and tetraploids produced similar numbers of bulbs (Fig. 2D), under solitary and intra-cytotype treatments. Diploids tended to produce more bulbs than tetraploids under inter-cytotype competition, but under interspecies competition this pattern was reversed, with tetraploids producing higher numbers of bulbs than diploids. Additionally, total change in bulb wet mass (Fig. 2E) did not differ between diploids and polyploids across all competition scenarios, except for interspecies competition where diploids had a much smaller increase in bulb mass than tetraploids.

Finally regarding seed production, although not part of the competition trial, seeds from legitimate intra-cytotype crosses showed clear size differences (Fig. 2F). Tetraploids produced larger seeds than diploids (p-value $= < 2 \times 10^{-16}$), with diploids averaging 1.88×10^{-4} g (SD $= 5.05 \times 10^{-5}$), and tetraploids 2.90×10^{-4} g (SD $= 6.57 \times 10^{-5}$).

Physiological traits

There were no significant main or interaction effect terms for any of the measured physiological traits (Rate of photosynthesis/CO_2 assimilation, Intrinsic water use efficiency and the Ratio of intercellular CO_2 to ambient CO_2) (Table 2).

Phenological traits

Only two traits exhibited significant differences: Number of days from emergence to final senescence and Number of days from first anthesis to last flower senescence (Table 2, Fig. 3). Diploids had an overall longer period above ground than tetraploids regardless of competition treatment (Fig. 3A). However, diploids also had a slightly longer flowering season than tetraploids under solitary or intra-cytotype competition, but under inter-cytotype and interspecies competition this difference between cytotypes became non-significant (Fig. 3B).

Discussion

The principle of competitive exclusion (Kneitel 2019) posits that two different species that occupy the same ecological niche and compete for the same available resources, cannot coexist indefinitely. Although now viewed as rather simplistic, this idea of competitive exclusion shaping species distribution patterns has been a cornerstone of ecological studies for many years, and indeed studies on community ecology often seek to reconcile these principles with mechanisms that may facilitate perceived coexistence among competitors (Kneital 2019). We can consider cytotypes of *O. obliquifolia* as being similarly subject to these same principles and paradoxes, since previous work has demonstrated that they are both phenotypically distinct and reproductively isolated in the wild (therefore behaving as separate species), and yet they appear to occupy the same abiotic niche and are generally co-occurring (Vaz de Sousa et al. 2024).

Our findings show that there are consistent phenotypic differences between diploids and tetraploids across a range of plant performance (including plant size and organ number) and functional traits (including slight phenological differences). Furthermore, there is no difference between growing cytotypes (both diploid and tetraploid) under solitary or intra-cytotype competition scenarios, over a broad suite of measured traits encompassing the entire plant. Furthermore, only two traits (Number of bulbs produced after one growing season and Number of days from first anthesis to last flower senescence) of 37 traits differed for cytotypes grown under intra-cytotype and inter-cytotype competition. With regards to the first trait, the response suggested a negative effect for tetraploid performance under inter-cytotype competition scenarios, whereas the second trait response suggested a potentially more negative effect for diploid performance under inter-cytotype competition scenarios. This is at odds with our expectations for cytotype sympatry under the Lotka–Volterra model of competition dynamics and principles of competitive exclusion, which suggest sympatry may be favoured where plant performance would be more negatively impacted by intra-cytotype competition effects than by inter-cytotype competition effects. Finally, there are four traits (both plant performance traits and functional traits) that differed when cytotypes are placed into competition with other species, which seem to generally disfavour diploids.

Morphological traits and tradeoffs

Unlike in many other southern-African *Oxalis* species (Becker et al. 2022), there is a distinct and largely consistent Gigas effect observed in *O. obliquifolia*, where polyploids tend to possess larger vegetative and reproductive organ structures, relative to diploids, which is consistent with previous work done on this species (Vaz de Sousa et al. 2024). The size differences between cytotypes also appear to be largely unaffected by the presence or type of competition. However, while size related traits did not show any significant response to changes in competition treatment, this is not the case when it comes to number-related traits.

Polyploids tended to produce fewer leaves and inflorescences than diploids, again consistent with the results observed in Vaz de Sousa et al. (2024). The inverse relationship between organ size and number suggests a possible tradeoff between these pairs of traits. The development of larger sized or higher numbers of organ structures, relative to diploids, would naturally require the allocation and investment of more available resources by the plant to the development of those organs (Huang et al. 2016). Theoretically an individual plant would not be able to maximally increase both organ size and number simultaneously, unless accessible resources are abundant enough to accommodate both. That polyploidy in this species, assuming similar/consistently limited resource availability and ability of cytotypes to utilise these resources, results in an increase in organ size, it would conversely necessitate a decrease in organ number. The assumption of similar ability of cytotypes to utilise available resources is justified in these results, since no significant differences in physiological traits (photosynthetic rate as an indicator of carbon accumulation) were observed between diploids and tetraploids. This further suggests that in this polyploid system, traits relating to the number of organ structures may be more impacted by changes in resource availability, and thus the effects of competition for those limited resources.

Cytotype competitive ability

A consistent finding in this study is that no trait (performance trait or functional trait) varied between solitary and intra-cytotype competition treatments, indicating that it is not the effect of competition itself, but specifically competition between diploids and polyploids, and interspecies competition, that impact plant performance/response. Furthermore, there is some evidence to suggest that tetraploids, with respect to their flowering phenology, appear to respond to

Table 2. Summary of generalised linear model results, for each of the uncorrelated and selected morphological, physiological and phenological traits assessed in the competition experiment, indicating the degrees of freedom, response variables and interaction terms after model simplification and associated p-values, and post hoc pairwise comparisons with associated Tukey adjusted p-values. *Indicates significant differences, threshold p-value = 0.05

				Post hoc pairwise comparisons	
Trait (units)	df	Response terms after model simplification	p-values	Pairs	Adjusted p-values
Morphological traits					
Above-ground traits					
Petiole length (mm)	57	Diploid (intercept)	–	Diploid vs Tetraploid	0.239
		Tetraploid	0.239		
Middle leaflet length (mm)	57	Diploid (intercept)	–	Diploid vs Tetraploid	4.14×10^{-5}*
		Tetraploid	4.14×10^{-5}*		
No. of leaves	57	Diploid solitary (intercept)	–	Diploid solitary vs Tetraploid solitary	2.00×10^{-4}*
				Diploid intra-cytotype vs Tetraploid intra-cytotype	2.90×10^{-3}*
		Tetraploid solitary	1.72×10^{-4}*	Diploid inter-cytotype vs Tetraploid inter-cytotype	1.38×10^{-2}*
				Diploid interspecies vs Tetraploid interspecies	0.697
		Diploid intra-cytotype	0.261	Diploid solitary vs Diploid intra-cytotype	0.675
				Diploid solitary vs Diploid inter-cytotype	0.923
		Diploid inter-cytotype	0.529	Diploid solitary vs Diploid interspecies	7.60×10^{-3}*
				Diploid intra-cytotype vs Diploid inter-cytotype	0.987
		Diploid interspecies	1.39×10^{-3}*	Diploid intra-cytotype vs Diploid interspecies	0.088
				Diploid inter-cytotype vs Diploid interspecies	0.098
		Tetraploid intra-cytotype	0.353	Tetraploid solitary vs Tetraploid intra-cytotype	0.995
				Tetraploid solitary vs Tetraploid inter-cytotype	0.992
		Tetraploid inter-cytotype	0.524	Tetraploid solitary vs Tetraploid interspecies	0.675
				Tetraploid intra-cytotype vs Tetraploid inter-cytotype	0.999
		Tetraploid interspecies	2.16×10^{-3}*	Tetraploid intra-cytotype vs Tetraploid interspecies	0.781
				Tetraploid inter-cytotype vs Tetraploid interspecies	0.879
Ratio petiole length to total plant height	57	Diploid (intercept)	–	Diploid vs Tetraploid	0.829
		Tetraploid	0.829		
Ratio middle leaflet length to middle leaflet width	57	Diploid (intercept)	–	Diploid vs Tetraploid	0.303
		Tetraploid	0.303		
Ratio lateral leaflet length to lateral leaflet width	57	Diploid (intercept)	–	Diploid vs Tetraploid	0.900
		Tetraploid	0.900		
Petal width (mm)	52	Diploid (intercept)	–	Diploid vs Tetraploid	3.52×10^{-5}*
		Tetraploid	3.52×10^{-5}*		
Bract length (mm)	52	Diploid (intercept)	–	Diploid vs Tetraploid	0.058
		Tetraploid	0.058		
Sepal width (mm)	52	Diploid (intercept)	–	Diploid vs Tetraploid	0.112
		Tetraploid	0.112		
Peduncle length (mm)	52	Diploid (intercept)	–	Diploid vs Tetraploid	1.28×10^{-2}*
		Tetraploid	1.28×10^{-2}*		
Ratio of flower diameter to petal length	52	Diploid (intercept)	–	Diploid vs Tetraploid	5.86×10^{-3}*
		Tetraploid	5.86×10^{-3}*		
Difference in peduncle and petiole lengths (mm)	52	Diploid (intercept)	–	Diploid vs Tetraploid	0.720
		Tetraploid	0.720		

(*continued*)

Table 2. Continued.

				Post hoc pairwise comparisons	
Trait (units)	df	Response terms after model simplification	p-values	Pairs	Adjusted p-values
No. of inflorescences	57	Diploid solitary (intercept)	–	Diploid solitary vs Tetraploid solitary	1.00×10^{-4}*
				Diploid intra-cytotype vs Tetraploid intra-cytotype	1.00×10^{-4}*
				Diploid inter-cytotype vs Tetraploid inter-cytotype	1.00×10^{-4}*
		Tetraploid	1.46×10^{-4}*	Diploid interspecies vs Tetraploid interspecies	1.00×10^{-4}*
				Diploid solitary vs Diploid intra-cytotype	0.720
				Diploid solitary vs Diploid inter-cytotype	0.974
		Diploid intra-cytotype	0.294	Diploid solitary vs Diploid interspecies	0.198
				Diploid intra-cytotype vs Diploid inter-cytotype	0.957
				Diploid intra-cytotype vs Diploid interspecies	0.734
		Diploid inter-cytotype	0.669	Diploid inter-cytotype vs Diploid interspecies	0.511
				Tetraploid solitary vs Tetraploid intra-cytotype	0.720
				Tetraploid solitary vs Tetraploid inter-cytotype	0.974
		Diploid interspecies	4.85×10^{-2}*	Tetraploid solitary vs Tetraploid interspecies	0.198
				Tetraploid intra-cytotype vs Tetraploid inter-cytotype	0.957
				Tetraploid intra-cytotype vs Tetraploid interspecies	0.734
				Tetraploid inter-cytotype vs Tetraploid interspecies	0.511
Below-ground traits					
No. of bulbs produced after one growing season	56	Diploid solitary (intercept)	-	Diploid solitary vs Tetraploid solitary	0.308
				Diploid intra-cytotype vs Tetraploid intra-cytotype	0.756
		Tetraploid solitary	0.308	Diploid inter-cytotype vs Tetraploid inter-cytotype	2.34×10^{-2}*
				Diploid interspecies vs Tetraploid interspecies	3.59×10^{-2}*
		Diploid intra-cytotype	0.495	Diploid solitary vs Diploid intra-cytotype	0.904
				Diploid solitary vs Diploid inter-cytotype	0.955
		Diploid inter-cytotype	0.606	Diploid solitary vs Diploid interspecies	0.211
				Diploid intra-cytotype vs Diploid inter-cytotype	0.631
		Diploid interspecies	0.052	Diploid intra-cytotype vs Diploid interspecies	0.457
				Diploid inter-cytotype vs Diploid interspecies	0.095
		Tetraploid intra-cytotype	0.582	Tetraploid solitary vs Tetraploid intra-cytotype	0.999
				Tetraploid solitary vs Tetraploid inter-cytotype	0.773
		Tetraploid inter-cytotype	0.283	Tetraploid solitary vs Tetraploid interspecies	0.655
				Tetraploid intra-cytotype vs Tetraploid inter-cytotype	0.674

(*continued*)

Table 2. Continued.

				Post hoc pairwise comparisons	
Trait (units)	df	Response terms after model simplification	p-values	Pairs	Adjusted p-values
		Tetraploid interspecies	2.65×10^{-2}*	Tetraploid intra-cytotype vs Tetraploid interspecies	0.725
				Tetraploid inter-cytotype vs Tetraploid interspecies	0.169
Largest bulb mass (g)	63	Diploid (intercept)	–	Diploid vs Tetraploid	0.595
		Tetraploid	0.595		
Change in total bulb mass (g)	63	Diploid solitary (intercept)	–	Diploid solitary vs Tetraploid solitary	0.266
				Diploid intra-cytotype vs Tetraploid intra-cytotype	0.466
		Tetraploid solitary	0.266	Diploid inter-cytotype vs Tetraploid inter-cytotype	0.092
				Diploid interspecies vs Tetraploid interspecies	2.96×10^{-2}*
		Diploid intra-cytotype	0.659	Diploid solitary vs Diploid intra-cytotype	0.971
				Diploid solitary vs Diploid inter-cytotype	0.807
		Diploid inter-cytotype	0.375	Diploid solitary vs Diploid interspecies	0.374
				Diploid intra-cytotype vs Diploid inter-cytotype	0.522
		Diploid interspecies	0.110	Diploid intra-cytotype vs Diploid interspecies	0.542
				Diploid inter-cytotype vs Diploid interspecies	0.093
		Tetraploid intra-cytotype	0.190	Tetraploid solitary vs Tetraploid intra-cytotype	0.518
				Tetraploid solitary vs Tetraploid inter-cytotype	0.999
		Tetraploid inter-cytotype	0.601	Tetraploid solitary vs Tetraploid interspecies	0.330
				Tetraploid intra-cytotype vs Tetraploid inter-cytotype	0.641
		Tetraploid interspecies	2.22×10^{-2}*	Tetraploid intra-cytotype vs Tetraploid interspecies	0.993
				Tetraploid inter-cytotype vs Tetraploid interspecies	0.454
Proportion of largest bulb mass to total bulb mass	63	Diploid (intercept)	–	Diploid vs Tetraploid	0.853
		Tetraploid	0.853		
Physiological traits					
Rate of photosynthesis/ CO_2 assimilation (μmol m^{-2} s^{-1})	54	Diploid (intercept)	–	Diploid vs Tetraploid	0.204
		Tetraploid	0.204		
Intrinsic water use efficiency (μmol_{CO2} $mol_{H2O}{}^{-1}$)	54	Diploid (intercept)	–	Diploid vs Tetraploid	0.780
		Tetraploid	0.780		
Ratio of intercellular CO_2 to ambient CO_2	54	Diploid (intercept)	–	Diploid vs Tetraploid	0.767
		Tetraploid	0.767		
Phenological traits					
Bulb survival	103	Diploid (intercept)	–	Diploid vs Tetraploid	0.909
		Tetraploid	0.909		
Plant emergence	109	Diploid (intercept)	–	Diploid vs Tetraploid	0.785
		Tetraploid	0.785		
No. of days to plant emergence	58	Diploid (intercept)	–	Diploid vs Tetraploid	0.513
		Tetraploid	0.513		
No. of days from emergence to final senescence	58	Diploid (intercept)	–	Diploid vs Tetraploid	4.53×10^{-2}*
		Tetraploid	4.53×10^{-2}*		
No. of days to first anthesis	54	Diploid (intercept)	–	Diploid vs Tetraploid	0.410
		Tetraploid	0.410		

(*continued*)

Table 2. Continued.

				Post hoc pairwise comparisons	
Trait (units)	df	Response terms after model simplification	p-values	Pairs	Adjusted p-values
No. of days from first anthesis to last flower senescence	54	Diploid solitary (intercept)	–	Diploid solitary vs Tetraploid solitary	2.00×10^{-3}*
				Diploid intra-cytotype vs Tetraploid intra-cytotype	1.37×10^{-2}*
		Tetraploid solitary	1.97×10^{-3}*	Diploid inter-cytotype vs Tetraploid inter-cytotype	0.447
				Diploid interspecies vs Tetraploid interspecies	0.895
		Diploid intra-cytotype	0.838	Diploid solitary vs Diploid intra-cytotype	0.997
				Diploid solitary vs Diploid inter-cytotype	0.580
		Diploid inter-cytotype	0.203	Diploid solitary vs Diploid interspecies	0.641
				Diploid intra-cytotype vs Diploid inter-cytotype	0.642
		Diploid interspecies	0.239	Diploid intra-cytotype vs Diploid interspecies	0.705
				Diploid inter-cytotype vs Diploid interspecies	0.999
		Tetraploid intra-cytotype	0.494	Tetraploid solitary vs Tetraploid intra-cytotype	0.880
				Tetraploid solitary vs Tetraploid inter-cytotype	0.105
		Tetraploid inter-cytotype	1.14×10^{-2}*	Tetraploid solitary vs Tetraploid interspecies	0.289
				Tetraploid intra-cytotype vs Tetraploid inter-cytotype	0.326
		Tetraploid interspecies	4.04×10^{-2}*	Tetraploid intra-cytotype vs Tetraploid interspecies	0.724
				Tetraploid inter-cytotype vs Tetraploid interspecies	0.816
No. of days from last flower senescence to plant senescence	54	Diploid (intercept)	–	Diploid vs Tetraploid	0.391
		Tetraploid	0.391		

interspecies competition and inter-cytotype competition in the same way, in other words they behave as if diploids were another species, and react by extending their flowering season to the same length as diploids. Additionally, diploids tended to show the larger negative response to interspecies competition, than tetraploids, by reducing their number of leaves, which might suggest that under these circumstances, tetraploids may possibly be the better interspecies competitor. This is since any compensation involving the organ size and organ number tradeoffs, afforded to diploids, may potentially be lost under interspecies competition.

While several previous studies have discussed the theory that differences in size between plants may translate into a competitive advantage for larger species (referred to as the size advantage hypothesis; Tracy and Aarssen 2014, Tracey et al. 2017), there is generally a lack of evidence for how this has shaped community-level organisation (Gridzak et al. 2024), and this may similarly be the case in diploid–polyploid complexes. However, tetraploids not only produce larger leaves and flowers, but also produced larger seeds than diploids, and this has the potential to translate into higher reproductive fitness, especially given previous work that showed no difference in the number of seed produced by diploids and tetraploids from intra-cytotype crosses (Vaz de Sousa et al. 2024). If seed size can be taken as an indication of seed/seedling advantage, this may translate into traits such as germination success, better survival during dormancy, and/or improved seedling vigour. Other studies (such as Stevens et al. 2020) have found that tetraploid seed, being both larger and heavier than diploid seeds, tend to confer an advantage to tetraploids, since their seeds have faster rates of germination, and that tetraploid seedlings tended to be both larger and grow faster than diploids. Tetraploids also tended to exhibit increased bulb dormancy, thereby allowing them to avoid germinating under conditions characterized by elevated abiotic stress (Stevens et al. 2020), along with potentially higher seed nutrient resources available to the developing seedling. However, these potential effects have not yet been assessed directly for this polyploid complex.

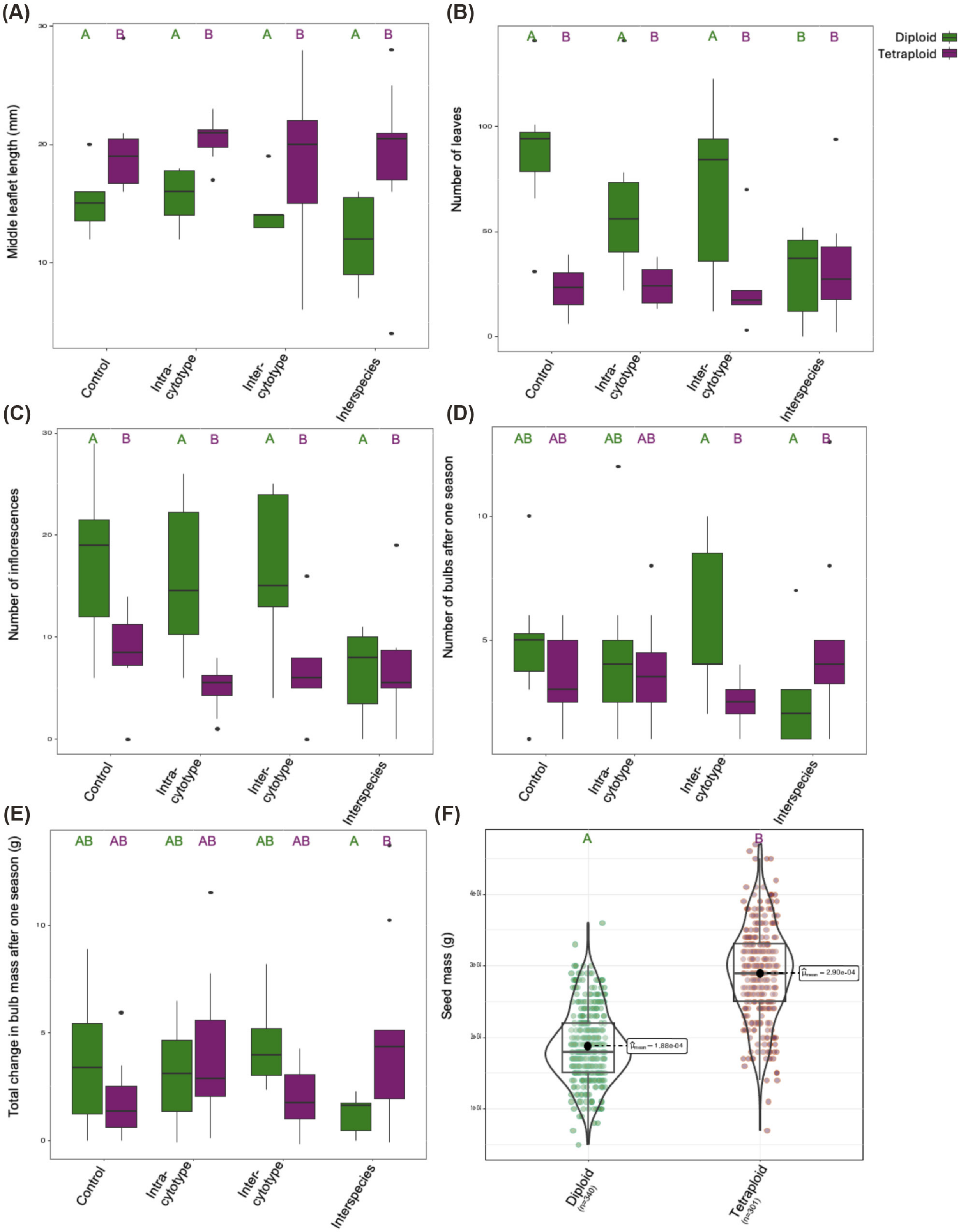

Figure 2. (A–E) Box-and-whisker plots of selected morphological traits measured for different cytotypes (diploids – green; tetraploids – purple) grown under controlled environmental conditions and under different types of competition (control/solitary plants; intra-cytotype; inter-cytotype; interspecies), and captured during the peak of the growing season. Traits include: (A) Middle leaflet length, (B) Number of leaves, (C) Number of inflorescences, (D) Number of bulbs after one season, and (E) Total change in bulb mass after one season. (F) Violin plot of seed masses for individual seed resulting from intra-cytotype crosses with solitary diploid and tetraploid parents, indicating mean seed mass. Letters above plots indicate statistically significant differences.

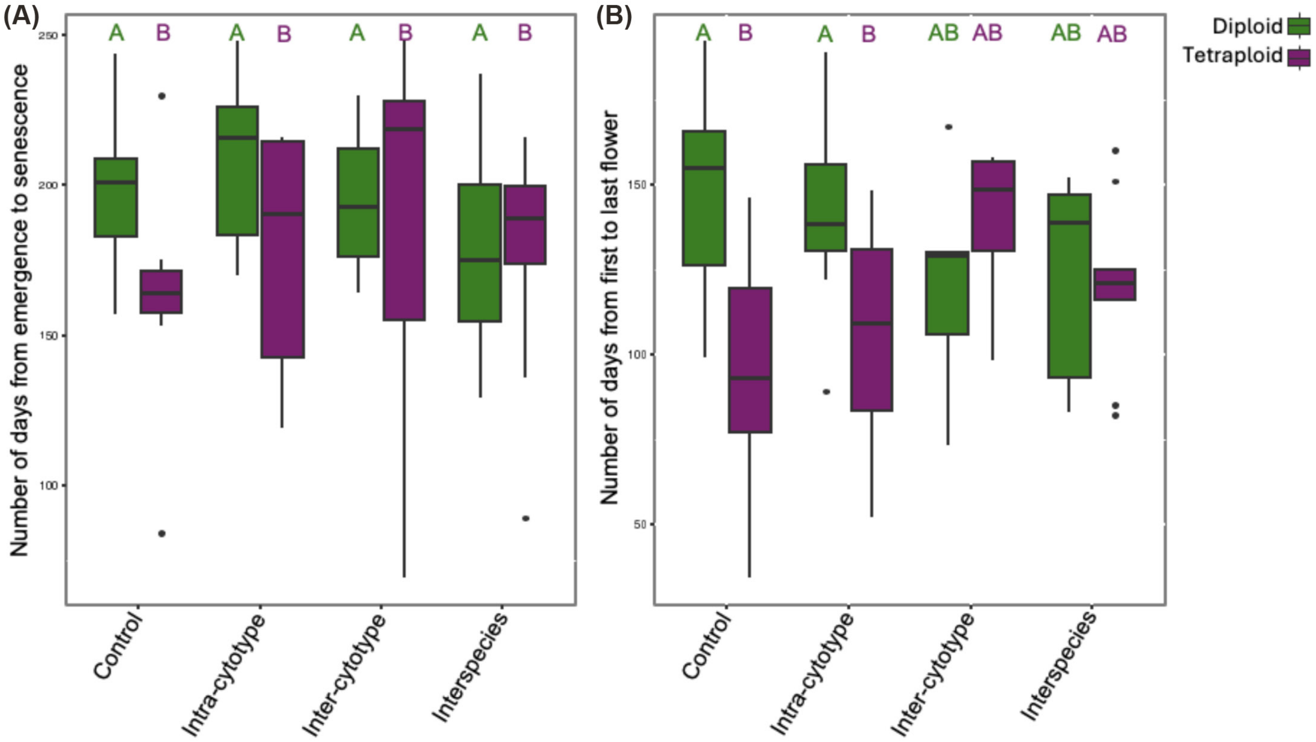

Figure 3. Box-and-whisker plots of selected phenological traits measured for different cytotypes (diploids – green; tetraploids – purple) grown under controlled environmental conditions and under different types of competition (control/solitary plants; intra-cytotype; inter-cytotype; interspecies), and captured over the duration of the trial. Letters above plots indicate statistically significant differences. Traits include: (A) Number of days from emergence to senescence, (B) Number of days from first to last flower.

Tetraploids also showed some evidence of higher increases in total bulb mass and bulb number under interspecies competition than diploids, however these effects appear to be subtle. Once again this may imply that tetraploids might fare better under interspecies competition scenarios, being able to not only accumulate more (wet) biomass at a faster rate than diploids, but also being able to produce higher numbers of vegetatively produced offspring. There is some evidence that effects of interspecies competition effects both above ground and below ground structures in similar ways, and in both cases diploids may be the more negatively impacted. There are a number of studies that have shown higher-level cytotypes with substantially higher capabilities for biomass accumulation (Chen 2010, Chae et al. 2013, Ardabili et al. 2015, Pacey et al. 2022) than diploid/lower-level cytotypes, and it also known that in many cases polyploids display an enhanced propensity for vegetative reproduction (Eckert et al. 2003, Duchoslav and Staňková 2015, Herben et al. 2017).

Tetraploid competitive advantage over diploids has been observed in other species, such as in *Jasione maritima* (Castro et al. 2023), but interestingly tetraploid advantage was only observed in neotetraploids, not in established polyploids, which were in fact more susceptible to negative competition effects. The authors suggested that post-polyploidisation selection may have had a role to play in the retention or loss of certain traits associated with competitive ability. The age of the *O. obliquifolia* polyploid lineage is unknown, so the role that post-polyploidisation selection may have played in this context cannot be quantified, but is a fertile area for future research.

Another study on *Chrysanthemum indicum* (Guo et al. 2023) found that tetraploids appeared to be the stronger competitor and that they were more negatively impacted by intra-cytotype competition effects with other tetraploids, as opposed to inter-cytotype competition effect with diploids. However, Guo et al. (2023) further showed that competition asymmetry amongst cytotypes was enhanced under abiotic stress conditions (in this case water availability), highlighting that competition effects are complex and likely to be altered by changes in abiotic conditions.

It is also possible that the overall lack of response by cytotypes, across most performance and functional traits, to intra-cytotype, and to a lesser extent inter-cytotype, competition may be because this species generally possesses overall weak competitive abilities, and only at higher densities may trait response to competition effects become more apparent. Guo et al. (2023) also discussed how the intensity of competition effects may be plant density dependent, and this was not a factor that was assessed in this study and may provide an explanation for why at the scale of interacting individuals (on a one to one basis) we do not observe large competition effects, until a much stronger competitor plant (in this case

Themeda triandra) was introduced. However, it is also possible that chance may have a role to play in the results of this investigation, given the number of tests, and so it must be acknowledged that caution must be taken when considering the results and their implications. Further testing and expanded studies may be necessary to ascertain the true validity of findings.

Unexpectedly, it is interesting that the degree of competition effect appears to vary negatively in response to the degree of the relationship between organisms, as noted by a reviewer. In other words, the more distantly related the competing organism the stronger the competition response from diploid and tetraploid plants. Future investigations should consider introducing additional competition treatments, including hexaploids (for other higher polyploidy cytotypes of differing relatedness to diploids and tetraploids) and other interacting species to test this idea.

Another interesting result from this investigation relates to the phenological traits associated with diploids and tetraploids. Generally, diploids were observed to have longer growing and flowering seasons than tetraploids, which is consistent with the findings in Vaz de Sousa et al. (2024), but these differences are only slight and generally cytotype growing and flowering seasons are extensively. Furthermore, the slightly longer growing season of diploids did not necessarily translate into higher increase in bulb biomass. However, the results suggest that while there is considerable overlap between diploids and tetraploids in different competition scenarios, tetraploids seem to extend their flowering time under inter-cytotype and interspecies competition scenarios, to the point that they are no longer significantly different to diploids. Another intriguing result is that diploids appear to produce far more bulbs than tetraploids under inter-cytotype competition. This immediately raises the question, why are cytotypes responding differently to competition with a different cytotype or species, yet seem unaffected by competition with like-cytotypes? What is the mechanism by which they can recognise and respond to these scenarios?

One possible explanation for this behaviour may be that diploids and tetraploids possess the ability to recognise kin (as has been observed in some other plant species; see Bais et al. 2006), or more closely related individuals. It has been shown that polyploid *O. obliquifolia* cytotypes in Gauteng (South Africa) are more closely related to each other than to diploids (Vaz de Sousa et al. 2024). One possible mechanism by which this kin recognition might be accomplished, for example, is through signalling by root interactions (reviewed by Bais et al. 2006), but this recognition is a largely unexplored possibility that is yet to be tested among different cytotypes in polyploid complexes.

Competition and cytogeography

Our results suggest that tetraploids may be the better interspecies competitor, since any compensation afforded to diploids by a tradeoff between having smaller but more numerous leaves and bulbils under inter-cytotype competition, is negated under interspecies competition scenarios. This apparent tetraploid advantage is further supported by an extended flowering season under both inter-cytotype and interspecies competition. Given these results, and based on the competitive exclusion principle, we would expect that diploids would gradually be out competed and displaced over time, by their more competitive polyploid counterparts. But again, this is inconsistent with the cytogeography observed in Vaz de Sousa et al. (2024).

If we accept the premise of competitive exclusion as being true, then one possible explanation for observed sympatry between reproductively isolated cytotypes may be that there is spatial segregation at finer scales than was included in previous assessments (i.e. they are in fact not sympatric at all but instead have a mosaic-like distribution of smaller parapatric groupings). To test this, one would have to conduct a far more thorough sampling at much finer scales, focusing on cytotype identification of closely occurring patches of *O. obliquifolia* plants (at the scale of just a few meters), and by documenting fine-scale local abiotic factors to assess for potential differences. Another possibility is that cooccurrence of cytotypes may be facilitated by ecological niche differentiation, other than long abiotic gradients. Indeed, there is some evidence to suggest that ecological niche differentiation may be enhanced under conditions where cytotypes are sympatric (Sonnleitner et al. 2015), thereby mitigating the effects of competition.

There is also the possibility that a mosaic-like distribution may result from stochastic effects, impacted by short distance ballistic dispersal of seed (Salter 1944), and the formation of vegetatively produced clonal plant patches that are often the case for this species. Such a process would result in cooccurrence and shared abiotic niche between cytotypes, in situations where competition between cytotypes is not strong enough to impact distribution or resource sharing (Gridzak et al. 2024), or while a state of equilibrium, under scenarios of competition asymmetry between cytotypes, has not yet been reached. The potential for non-equilibrium systems to change over time is a factor that cannot be overlooked, and indeed long-term monitoring of distributions are among the few ways we would be able to assess these dynamics. However, there is another factor to consider when it comes to changes in cytogeographic patterns, and that involves the role of changing environments, historically (Casazza et al. 2012), as well as the effects that future climate stress (Guo et al. 2023) may have on polyploid complexes more generally, and more specifically on cytotype competition dynamics.

Conclusion

The effects of polyploidisation on plant morphology and ecophysiology has been the topic of many studies over the last few decades, however, many of our assumptions about the potential effects of polyploidy for plant ecology, specifically regarding plant competitive ability, are based on studies focused on plants grown under solitary conditions. Very few studies have directly assessed cytotype competitive ability using competition treatments. In this study we used competition experiments to test for differences in competitive ability between diploids and tetraploids of *Oxalis obliquifolia* and showed that cytotypes indeed respond idiosyncratically under different competition scenarios, and more specifically that tetraploids may potentially be better interspecies competitors than diploids.

These findings are not straightforward to interpret, given the high degree of sympatry observed in this species. These suggest other underlying explanations or mechanisms may be shaping the cytogeography of this polyploid complex and presents us with several possible avenues for further investigation. One interesting outcome of this study is that cytotypes respond differently to competition with like cytotypes, competition with other cytotypes, and interspecific competition, which raises the question of how they make the distinction.

Finally, it must also be emphasised that these trials were conducted under controlled abiotic conditions. How might abiotic stress under field conditions influence these dynamics, especially under future climate scenarios?

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Permits – It is hereby confirmed that all ethical clearance standards and criteria were fulfilled for the execution of this work and that ethical clearance was duly granted by the host research institution (University of Pretoria; ethical clearance number: DePSS-ethics-2024-DVKO).

Author contributions

Damian Vaz de Sousa: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (lead); Writing – review and editing (equal). **Michelle Greve**: Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Writing – review and editing (equal). **Nicolette J. Taylor**: Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Kenneth C. Oberlander**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from Figshare: https://doi.org/10.25403/UPresearchdata.29164067 (Vaz de Sousa et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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