

Research article

Investigating the effects of whole genome duplication on phenotypic plasticity: implications for the invasion success of giant goldenrod *Solidago gigantea*Angela M. Walczyk^{1,2} and Erika I. Hersch-Green¹¹Department of Biological Sciences, Michigan Technological University, Houghton, MI, USA²Biology Department, Gustavus Adolphus College, St. Peter, MN, USACorrespondence: Angela M. Walczyk (awalczyk@gustavus.edu)

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Polyploidy commonly occurs in invasive species, and phenotypic plasticity (PP, the ability to alter one's phenotype in different environments) is predicted to be enhanced in polyploids and to contribute to their invasive success. However, empirical support that increased PP is frequent in polyploids and/or confers invasive success is limited. Here, we investigated if polyploids are more pre-adapted to become invasive than diploids via the scaling of trait values and PP with ploidy level, and if post-introduction selection has led to a divergence in trait values and PP responses between native- and non-native cytotypes. We grew diploid, tetraploid (from both native North American and non-native European ranges), and hexaploid *Solidago gigantea* in pots outside with low, medium, and high soil nitrogen and phosphorus (NP) amendments, and measured traits related to growth, asexual reproduction, physiology, and insects/pathogen resistance. Overall, we found little evidence to suggest that polyploidy and post-introduction selection shaped mean trait and PP responses. When we compared diploids to tetraploids (as their introduction into Europe was more likely than hexaploids) we found that tetraploids had greater pathogen resistance, photosynthetic capacities, and water-use efficiencies and generally performed better under NP enrichments. Furthermore, tetraploids invested more into roots than shoots in low NP and more into shoots than roots in high NP, and this resource strategy is beneficial under variable NP conditions. Lastly, native tetraploids exhibited greater plasticity in biomass accumulation, clonal-ramet production, and water-use efficiency. Cumulatively, tetraploid *S. gigantea* possesses traits that might have predisposed and enabled them to become successful invaders. Our findings highlight that trait expression and invasive species dynamics are nuanced, while also providing insight into the invasion success and cyto-geographic patterning of *S. gigantea* that can be broadly applied to other invasive species with polyploid complexes.

Keywords: Invasive species, nitrogen, nutrients, phenotypic plasticity, phosphorus, photosynthesis, polyploidy

Introduction

Phenotypic plasticity (PP), the ability of a single genotype to change its phenotype in response to environmental changes (Pigliucci et al. 2006, Fusco and Minelli 2010, Gianoli and Valladares 2012), is suspected to promote invasive species success for two main reasons. First, invaders are usually exposed to novel environments (e.g. new climates, enemies and/or competitors) upon introduction and enhanced PP could allow them to better tolerate these novel conditions while maintaining fitness before fixed adaptations occur (Agrawal et al. 2008, Chevin et al. 2010, Gratani 2014, Colautti et al. 2017, Fox et al. 2019). Second, new invading populations often suffer from low genetic diversity and associated inbreeding depression (e.g. bottleneck effects, inbreeding depression; Charlesworth and Willis 2009, Rosche et al. 2016), and PP could enhance a population's phenotypic variation, and thus ability to respond to novel environments, despite initially having reduced genetic diversity (Pérez et al. 2006, Ardura et al. 2017). Although theoretically plausible, empirical evidence supporting the occurrence and/or importance of PP towards successful biological invasions is mixed with invasive populations being more (Porté et al. 2011, Knop and Reusser 2012, Matesanz et al. 2012, Luo et al. 2019, Bufford and Hulme 2021), less (Lamarque et al. 2013, Wang et al. 2018, Plantamp et al. 2019, Albarrán-Mélzer et al. 2020), or equally (Peperkorn et al. 2005, Palacio-López and Gianoli 2011, Matzek 2012, Ryan and Gunderson 2021) plastic relative to non-invasive populations. While such discrepancies in our understanding of PP in invasive systems are likely due to differences in experimental methodology, genotypes used, traits measured, and/or environments examined among studies (Pichancourt et al. 2012, Van Wallendael et al. 2018, Amat-Trigo et al. 2019, Granata et al. 2020), the ploidy level of an invading species might also be an important defining characteristic to consider in understanding whether and how PP influences invasive success.

Polyploidy, the state of containing three or more chromosome sets per cell, is a common attribute of many successful and ecologically devastating invasive plant species (Pyšek and Richardson 2010, Pandit et al. 2011, Te Beest et al. 2012, Suda et al. 2015). The invasive success of polyploids has been attributed to morphological, chemical, and/or physiological trait changes induced by polyploidy (McIntyre 2012, Chao et al. 2013, Ramsey and Ramsey 2014) that alter ecological interactions (Van de Peer et al. 2017, 2021), environmental tolerances (Mráz et al. 2014), resilience to inbreeding depression (Rosche et al. 2018), and fitness or persistence traits (Collins et al. 2011) in ways that predispose organisms to be more successful invaders (Pandit et al. 2006, 2011, Te Beest et al. 2012, Van de Peer et al. 2017, 2021, Wani et al. 2018). Furthermore, it has also been suggested that polyploidy is associated with enhanced PP capacity in traits that can promote and predispose organisms to succeed in novel environments (Jackson and Chen 2010, Gallego-Tévar et al. 2018, Noble et al. 2019, Wei et al. 2019, Landy et al. 2020). Increased PP in polyploids is

thought to arise from a combination of increased genomic and genetic variability (Comai 2005, Chen 2010, Soltis et al. 2015, Vogt 2017, Ding and Chen 2018, Doyle and Coate 2019), and changes in gene expression and dosage effects (Bastiaanse et al. 2019); both of which follow polyploidization events (Sémon and Wolfe 2007, Soltis et al. 2015, Ding and Chen 2018, Doyle and Coate 2019) and may offer genotypes more phenotypic flexibility. Although changes in trait means or PP responses induced by polyploidy may pre-adapt organisms to be more successful invaders (Jackson and Chen 2010, Gallego-Tévar et al. 2018, Wei et al. 2019), it is also possible that increased genetic diversity and redundancy following whole genome duplication might expedite adaptation occurring post-introduction and select for traits and/or increased plasticity responses that favor success in novel environments. For instance, several studies have reported a shift in investment from defensive to competitive traits in invasive genotypes, potentially owing to reduced selection pressures from specialist antagonists in novel ranges (i.e. evolution of increased competitive ability hypothesis; Blossey and Notzold 1995, Vilà et al. 2005, Liu et al. 2007, Correia et al. 2016, Hartshorn et al. 2022). Despite these strong theoretical frameworks and possibilities, polyploids have been shown to be more (e.g. invasive populations: Hahn et al. 2012, Rejlová et al. 2019), less (e.g. invasive populations: Harms et al. 2021; native populations: Wei et al. 2019, Kornstad et al. 2022), and equally (e.g. native populations: Sánchez Vilas and Pannell 2017) phenotypically plastic than related diploid genotypes.

Here, our main objectives were to determine 1) if trait values and PP increase with ploidy level, 2) if the invasive cytotype within a species complex possesses traits and PP responses that convey pre-adaptive invasive advantages over other cytotypes, and 3) if selective forces post-introduction have led to trait and PP response divergence between an invasive cytotype and its native counterpart. We used *S. gigantea*, a perennial autopolyploid complex native to North America but highly invasive in Eurasia (Schlaepfer et al. 2008, 2010), to address these objectives by examining how traits thought to be related to invasive species success respond to changes in soil nitrogen (N) and phosphorus (P) levels. Because sufficient soil nutrients are important for plant growth and fitness, soil nutrient availability is likely to exert strong selective pressure on invasive success and patterns of PP (Davis et al. 2000, Pearson et al. 2018). Furthermore, biological invasions usually begin in urbanized areas with elevated levels of biologically available N and P (Penuelas et al. 2013, Fowler et al. 2015, Goyette et al. 2016, Asabere et al. 2018), and we reasoned that this would be a relevant novel environment to explore. Specifically, we grew diploid and polyploid *S. gigantea* geo-cytotypes collected from their native (diploid, tetraploid, hexaploid) and invasive (tetraploid only) ranges under low, medium, or high soil NP conditions in pots placed outside to address three general predictions. First, we predicted that both mean trait and PP values would correlate positively with ploidy level (due to increased genomic and genetic content and flexibility; Sémon and Wolfe 2007, Soltis et al. 2015,

Ding and Chen 2018, Doyle and Coate 2019) and that the degree of difference between cytotypes' PP and direction of trait mean changes would depend upon environmental shifts in soil nutrients. Polyploids are hypothesized to require more N and P atoms to build and maintain their larger genomes and cells (Beaulieu et al. 2008, Elser et al. 2011, Mueller 2015) and have been shown to be more growth and fitness limited by N and P availabilities than diploids (Hessen et al. 2013, Neiman et al. 2013, Šmarda et al. 2013, Guignard et al. 2016, Bales and Hersch-Green 2019, Walczyk and Hersch-Green 2019, 2022, Anneberg and Segraves 2020, Peng et al. 2022). Therefore, we predicted that when polyploids are no longer constrained by nutrients, they would invest more into other processes (Faizullah et al. 2021), such as growth and defense, subsequently increasing trait means and elevating PP (which was calculated as the difference in trait expression for maternal lines between environments; Pigliucci et al. 2006, Agrawal et al. 2008, Gianoli and Valladares 2012). Second, and related to the above, we specifically hypothesized that native tetraploids possess traits and PP responses that pre-adapt them to be the most invasive cytotype of *S. gigantea* given their current invasive status. Lastly, we predicted that invasive European tetraploids would exhibit greater PP responses for traits related to invasive success than native North American tetraploids, as enhanced plasticity for traits that confer greater competitive advantages or fitness allow individuals to better tolerate novel and/or variable environmental pressures and would have been selectively favored (Pigliucci et al. 2006, Fusco and Minelli 2010, Gianoli and Valladares 2012).

Material and methods

Model species

Giant goldenrod *Solidago gigantea* (Asteraceae) is a widespread, insect-pollinated, perennial autopolyploid complex (Beck and Semple, pers. comm.) that successfully establishes new populations through seed dispersal and rhizomatous growth (Weber and Jakobs 2005). In its native range of North America, it occurs as three spatially distinct geo-cytotypes: diploid ($2n=2x=18$) populations are found along the Atlantic coast, tetraploid populations ($2n=4x=36$) are found within the Great Lakes region, and hexaploid populations ($2n=6x=54$) are found within the Great Plains region (Schlaepfer et al. 2008, 2010, Hull-Sanders et al. 2009, Martino et al. 2020). Only tetraploid cytotypes are found in parts of Eurasia (Schlaepfer et al. 2008, 2010), where it is an exotic and highly invasive species that negatively affects local plant (Weber and Jakobs 2005) and soil microbial communities (Bobulská et al. 2019). Cytotypes and geographically separated populations show phenotypic (Martino et al. 2020) and genetic (i.e. increases with ploidy level; Nagy et al. 2018) differences, owing to shifts in niche space and tolerances following whole genome duplication (Nagy et al. 2018, Martino et al. 2020). Native and exotic tetraploid

environments are also likely to differ in many ways. For instance, within its native range, *S. gigantea* is damaged by many specialists and generalist invertebrate herbivores, while within its non-native range, *S. gigantea* is only damaged by a few invertebrate generalist herbivores (Jakobs et al. 2004, Weber and Jakobs 2005).

Plant sampling

During the summers of 2017 to 2019, we collected seeds from 10 individual plants that were spaced at least 10 m apart from 21 populations across *S. gigantea*'s native range and from 15 populations in its invasive range (all near Zurich, Switzerland; see Supporting information for site coordinates). We also collected 2–3 leaves from 20 individual plants that were also spaced at least 10 m apart per population, immediately dried them in silica gel, and used flow cytometry methods to determine the ploidy level of plants (following the protocol of Walczyk and Hersch-Green 2022). After confirming an absence of mixed-ploidy populations, which rarely occurs in *S. gigantea* (Schlaepfer et al. 2008, 2010, Hull-Sanders et al. 2009, Martino et al. 2020), we selected maternal plants as seed sources that came from populations composed of a single geo-cytotype (Supporting information).

Experimental design

We germinated seeds from six biological replicates from four half-sibling maternal lines (i.e. seeds collected from the same plant) collected from three populations per geo-cytotype (native diploids, tetraploids, and hexaploids and invasive tetraploids; $n=72$ per geo-cytotype or 288 plants total) in seed trays in a greenhouse under 16:8 h light:dark cycle at Michigan Technological University (Houghton, Michigan, USA). After two weeks, plants were transplanted to 7.6-l round pots containing a 50:50 mixture of vermiculite to Sun Grow Mix 1 potting soil and pots were randomly arranged in an open field on the campus of Michigan Technological University where they received one of three NP treatments (low, medium, high; $n=24$ per geo-cytotype per treatment). Because the potting soil already contained 110 ppm N ($\mu\text{g N g}^{-1}$) and 25 ppm P ($\mu\text{g P g}^{-1}$), we designated this as the low treatment and we added nutrients to medium- and high-treatment plots to represent two levels of nutrient deposition 'hotspots' common to urban environments (Bettez and Groffman 2013, Rao et al. 2014). We designated the medium-NP treatment as 165 ppm N ($\mu\text{g N g}^{-1}$) and 37.5 ppm P ($\mu\text{g P g}^{-1}$; $1.5\times$ increase from low treatment) and the high-NP treatment as 220 ppm N ($\mu\text{g N g}^{-1}$) and 50 ppm P ($\mu\text{g P g}^{-1}$; $2\times$ increase from low treatment). All treatments were administered as 50 ml solutions composed of ammonium nitrate and potassium monophosphate or plain water (low treatments) plus 100 ppm of potassium sulfate ($\mu\text{g K g}^{-1}$) and 3.22 ml micronutrients (Fertilome chelated liquid iron and other micronutrients). Plants received 50 ml treatment doses three times throughout the course of the experiment on weeks 2, 6 and 10 of experimental growth, were

exposed to natural precipitation and temperatures, and were watered equally as needed. The experiment ran for 21 weeks from early June to early October 2020.

Measured traits

We measured mean values and PP responses of traits associated with growth, reproduction, physiology, and resistance to antagonists, because these traits are likely to be important for species success in novel environments.

Growth traits

Above- and belowground biomasses can influence plant competitive ability for light, space, water, and soil nutrients, with larger biomasses typically displaying greater competitiveness (Aerts 1999, Craine and Dybzinski 2013), which could contribute to invasive species success (Schultheis and MacGuigan 2018). At harvest, plants were severed at the soil line and separated into their above- and belowground parts, dried in a drying oven (48 h for aboveground, 72 h for belowground), and weighed. From these values we also calculated the root:shoot ratio (R:S ratio) because this ratio can be indicative of nutrient investments into current versus future reproductive potential and resource acquisition strategies (both indicated by low R:S ratios; Gioria and Osborne 2014, Goldberg et al. 2017), both of which also might contribute to invasive establishment and spread (Wilsey and Polley 2006, Heberling and Fridley 2013).

Reproductive traits

Clonality is a metric of asexual fitness and is thought to promote invasive species success by allowing organisms to persist despite initially lacking sexual partners (Dong et al. 2014, Yu et al. 2016). At harvest, we therefore counted the number of clonal ramets (i.e. genetically identical vegetative growths attached to a 'parent plant' that have the potential to flower; Dong et al. 2014). Because most plants failed to flower during experimentation, we were unable to also obtain a metric of sexual reproduction.

Physiological traits

Strategies that enhance plant performance and competitive ability via high photosynthetic activity and/or water conservation are also associated with the establishment and spread of invasive species (McDowell 2002, Rindyastuti et al. 2021). Therefore, we decided to measure maximum carbon assimilation rate ($A_{\max}$, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and instantaneous water use efficiency (WUE_i ; Medrano et al. 2015) of 144 plants ($n=12$ per geo-cytotype per treatment). We measured $A_{\max}$ and evapotranspiration (E) rates with a portable infrared CO_2 analyzer system equipped with a CO_2 mixer and $1 \times 3 \text{ cm}^2$ chamber/red-blue LED light source (LI6800-02) with the following conditions set in the inside chamber: CO_2 concentration = 400 ppm, relative humidity = 65%, flow rate = 500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, light = 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. All measurements were taken once photosynthetic rates stabilized on the youngest, fully developed leaf on a plant, in a random order

spread over two sampling days within the hours of 09:00 to 16:00 during the 10th and 14th week of growth and infrared gas analyzers (IRGAs) were matched between plants. We obtained WUE_i by dividing $A_{\max}$ by E .

Antagonist resistance traits

Damage by insect herbivores and pathogens can negatively affect plant fitness (Herrera et al. 2002, Erb 2018), and resistance to these antagonists can vary among ploidy levels (Thompson et al. 1997, Nuismer and Thompson 2001, Segraves and Anneberg 2016) and between populations from native versus invasive ranges (Bosddorf et al. 2005, Huang et al. 2010). To assess whether polyploidy and/or selection within a part of the non-native range has altered resistance patterns we quantified plant leaf damage mid-season by counting the number of leaves on each plant showing damage by naturally occurring insect herbivores (e.g. chewing, mining, sap-sucking) and/or pathogens (e.g. discoloration, fungal rust) and then divided these numbers by the total number of leaves. Resistance to insect and pathogen foliar damage was then calculated by subtracting the percent of insect- and pathogen-damaged leaves from a value of '1,' respectively (Rauscher and Simms 1989, Fornoni et al. 2004).

Statistics

All statistical models consisted of a combination of the following fixed-effect independent factors: geo-cytotype ($2x$ =diploid, $4x^N$ =North American tetraploid, $4x^E$ =European tetraploid, $6x$ =hexaploid), NP treatment (L =low, M =medium, H =high), nutrient-level change (low to medium, medium to high), and/or population of origin (nested within 'geo-cytotype'). We examined correlations between measured trait and PP values, and if values were found to be highly correlated (i.e. correlation greater than 0.60; Johnson and Wichern 2002, Hair et al. 2006) we used MANOVA models to reduce the likelihood of type I errors. We checked model assumptions of normality and homoscedasticity and made data transformations as needed. When geo-cytotype or an interaction involving geo-cytotypes were found to be significant we used two controlled contrasts to test for significant differences among 1) North American cytotypes ($2x$, $4x^N$, $6x$) and 2) North American versus European tetraploids ($4x^N$, $4x^E$); and, when NP treatment was found to be significant, we used Tukey's HSD analysis to test for significant differences among NP treatment means. All statistical analyses were performed using JMP Pro ver. 16 (SAS Instit.).

Trait level differences

Because of high correlations between above- and belowground biomasses and clonal ramets (Johnson and Wichern 2002, Hair et al. 2006, Supporting information), we used a MANOVA model (with an identity response) to test whether geo-cytotype, nutrient treatment, their interactions, and/or population of origin (nested within geo-cytotype)

significantly affected aboveground biomass, belowground biomass, and the number of clonal ramets produced by a plant. Because the overall MANOVA model and independent factors within the MANOVA model were found to be significant (Table 1), we also performed separate univariate ANOVA models for each of these three traits to examine significant differences among factor-level means. Owing to low correlations between traits (Supporting information) we used separate ANOVA models to examine whether R:S ratio (square-root transformed), $A_{\max}$, WUE_p , insect resistance ($\log(x+1)$ transformed), and/or pathogen resistance significantly differed among geo-cytotypes, nutrient treatments, their interactions, and/or population (nested within geo-cytotype).

Phenotypic plasticity differences

To calculate PP, we created reaction norm plots (Pigliucci et al. 2006, Agrawal et al. 2008, Gianoli and Valladares 2012) by first averaging trait values of each maternal line per geo-cytotype separately for each NP treatment and then plotting these averaged values from each maternal line across the three NP treatments. Next, the absolute value of the slope of the line between two nutrient treatment pairs was taken as the PP metric (Arnold et al. 2019), where a zero-slope indicates an absence of PP and larger slope values correspond to greater PP. Correlation values between trait PP metrics were low (Johnson and Wichern 2002, Hair et al. 2006, Supporting information), so we used univariate models to statistically assess PP patterns. We used separate ANOVA models to examine whether PP values for aboveground biomass, belowground biomass, R:S ratio (square-root transformed), the number of clonal ramets, $A_{\max}$, WUE_p , insect resistance, and/or pathogen resistance significantly differed among geo-cytotypes, nutrient-level changes (low-medium, medium-high), their interactions, and/or population of origin (nested within geo-cytotype). We failed to measure biomass-related traits on one European tetraploid and one hexaploid, and the physiology-related traits on two European tetraploids, and thus data from these plants, were not included in subsequent statistical analyses.

Results

Growth traits

Population of origin and NP treatment significantly affected biomasses, and geo-cytotype had a significant effect on aboveground biomass, although differences in both above- and belowground biomasses among geo-cytotypes depended upon NP treatment (Table 1). Generally, plants had greater biomasses with increasing NP levels, and under low NP conditions geo-cytotypes did not differ from each other (Table 2, Fig. 1). However, in medium-NP treatments, diploid and native tetraploids had greater biomasses than hexaploids (although tetraploid belowground biomass did not significantly differ from the other two cytotypes; Table 2, Fig. 1). Furthermore, in high-NP treatments, native tetraploids had greater aboveground biomasses than diploids and hexaploids, but lower belowground biomasses than hexaploids (Table 2, Fig. 1). Among the two regional tetraploids in medium-NP treatments, North American tetraploids had significantly greater above- and belowground biomasses than European tetraploids, and in the high-NP treatments, they also had greater aboveground biomass than the European tetraploids (Table 2, Fig. 1).

PP values for above- and belowground biomasses significantly differed among geo-cytotypes, but only dependent upon nutrient level treatment changes (Table 3). Within native cytotypes, when nutrients increased from low to medium treatments, both diploids and tetraploids were more plastic for aboveground biomass accumulation than hexaploids (e.g. they increased their biomass more; Table 4, Fig. 1, 2A). Whereas for belowground biomass, diploids were the most, tetraploids intermediate, and hexaploids the least plastic (Table 4, Fig. 1, 2B). In contrast, within the native cytotypes the reverse pattern for above- and belowground biomass emerged when nutrients increased from medium to high. Specifically, hexaploids were the most, tetraploids intermediate, and diploids the least plastic for aboveground biomass, and tetraploids and diploids both had significantly less belowground plasticity than hexaploids (Table 4, Fig. 1, 2A). Among the two regional tetraploids, North American tetraploids significantly increased their above- and belowground

Table 1. Results of MANOVA and univariate ANOVA models testing whether geo-cytotype (diploid = 2x, North American tetraploid = 4x^N, European tetraploid = 4x^E, hexaploid = 6x), soil NP treatment (L = low, M = medium, H = high), their interaction, and/or geo-cytotype nested within population of origin affected mean values of growth and reproductive traits (aboveground biomass, belowground biomass, and clonal ramet production). The Wilk's lambda (MANOVA) and R² (ANOVA) values for the whole models are listed and bold values indicate a significant effect at $\alpha = 0.05$.

Independent factors	MANOVA model results				Univariate ANOVA results					
					Aboveground biomass			Belowground biomass		No. of clonal ramets
	df _n , df _d	F	p-value	df ₁ , df ₂	F	p-value	F	p-value	F	p-value
Geo-cytotype (C)	9, 645	6.23	< 0.0001	3, 267	5.54	0.0010	1.91	0.1280	8.81	< 0.0001
NP treatment (NP)	6, 530	65.17	< 0.0001	2, 267	226.14	< 0.0001	155.03	< 0.0001	75.52	< 0.0001
C x NP	18, 750	3.31	< 0.0001	6, 267	6.30	< 0.0001	4.32	0.0004	1.26	0.2742
Population [C]	24, 769	4.62	< 0.0001	8, 267	8.15	< 0.0001	5.98	< 0.0001	4.52	< 0.0001
Whole model	57, 791	9.80	< 0.0001	19, 267	29.88	< 0.0001	20.41	< 0.0001	11.62	< 0.0001

Table 2. Results of controlled contrast post hoc tests for significant model factors 'geo-cytotype × nutrient treatment' and 'geo-cytotype' for mean trait values (see Table 1, 5). These controlled contrasts were used to test whether there were significant differences between native cytotypes (diploids (2x), North American tetraploids (4x^N), and hexaploids (6x)), and/or between regional tetraploids (North American tetraploids (4x^N) and European tetraploids (4x^E)) within or independent of NP treatments. Bold values indicate a significant effect at $\alpha=0.05$. NP=nitrogen and phosphorus.

	F _(df1,df2)	Prob > F	t-test results
Within geo-cytotype × NP treatment			
Aboveground biomass			
Low NP for native cytotypes	1.31 _(2,267)	0.2721	
Low NP for regional tetraploids	0.52 _(1,267)	0.4721	
Medium NP for native cytotypes	15.53 _(2,267)	< 0.0001	4x ^N = 2x > 6x
Medium NP regional tetraploids	11.13 _(1,267)	0.0010	4x ^N > 4x ^E
High NP for native cytotypes	4.78 _(2,267)	0.0091	4x ^N > 2x = 6x
High NP regional tetraploids	11.40 _(1,267)	0.0008	4x ^N > 4x ^E
Belowground biomass			
Low NP for native cytotypes	2.66 _(2,267)	0.0721	
Low NP for regional tetraploids	0.77 _(1,267)	0.3805	
Medium NP for native cytotypes	4.68 _(2,267)	0.0101	2x (= 4x ^N) > 6x (= 4x ^N)
Medium NP regional tetraploids	4.28 _(1,267)	0.0396	4x ^N > 4x ^E
High NP for native cytotypes	3.69 _(2,267)	0.0263	6x (= 2x) > 4x ^N (= 2x)
High NP regional tetraploids	0.01 _(1,267)	0.8989	
R:S ratio			
Low NP for native cytotypes	6.80 _(2,265)	0.0013	4x ^N = 6x > 2x
Low NP for regional tetraploids	0.42 _(1,265)	0.5175	
Medium NP for native cytotypes	4.53 _(2,265)	0.0016	6x (= 4x ^N) > 2x (= 4x ^N)
Medium NP regional tetraploids	0.13 _(1,265)	0.7226	
High NP for native cytotypes	6.74 _(2,265)	0.0014	2x = 6x > 4x ^N
High NP regional tetraploids	2.75 _(1,265)	0.0986	
Within geo-cytotype			
Clonal ramets			
Native cytotypes	13.09 _(2,267)	< 0.0001	4x ^N = 2x > 6x
Regional tetraploids	4.19 _(1,267)	0.0418	4x ^N > 4x ^E
A_{max}			
Native cytotypes	30.13 _(2,267)	< 0.0001	6x > 4x ^N > 2x
Regional tetraploids	3.34 _(1,267)	0.0688	
WUE_i			
Native cytotypes	13.90 _(2,267)	< 0.0001	6x = 4x ^N > 2x
Regional tetraploids	17.17 _(1,267)	< 0.0001	4x ^N > 4x ^E
Leaf pathogen resistance			
Native cytotypes	27.70 _(2,267)	< 0.0001	6x > 4x ^N > 2x
Regional tetraploids	1.09 _(1,267)	0.2980	

biomass more (e.g. had higher PP values) than European tetraploids, but only when nutrients increased from low to medium and not when nutrients increased from medium to high, in which case the geo-cytotypes did not significantly differ from each other (Table 4, Fig. 1, 2).

Population of origin, geo-cytotype, and NP treatment each significantly affected R:S ratios, but differences in R:S ratios among geo-cytotypes depended upon NP treatment (Table 5). In general, plants tended to invest more into aboveground relative to belowground biomass (i.e. had smaller mean R:S ratios) as NP enrichment increased (untransformed R:S ratio LSMeans $\pm$ 1SE under low NP = 2.94 $\pm$ 0.11, medium NP = 2.85 $\pm$ 0.11, high NP = 2.60 $\pm$ 0.11). But, for only the native cytotypes, patterns and significance varied among NP treatments (Table 2). For instance, under low-NP conditions tetraploids invested significantly more into belowground relative to aboveground biomass than diploids, while hexaploids were intermediate (Table 2; untransformed R:S ratio LSMeans $\pm$ 1SE for 2x = 2.27 $\pm$ 0.35, 4x^N = 3.69 $\pm$

0.35, 6x = 3.34 $\pm$ 0.35). Whereas under high NP conditions, diploids and hexaploids both invested significantly more into belowground relative to aboveground biomass than tetraploids (untransformed LSMeans $\pm$ 1SE R:S ratios for 2x = 2.73 $\pm$ 0.35, 4x^N = 2.09 $\pm$ 0.35, 6x = 3.15 $\pm$ 0.35; Table 2). No model factors nor interactions among model factors influenced R:S plasticity responses (Table 3).

Asexual reproduction

The number of clonal ramets produced by a plant significantly varied depending upon population of origin and the individual effects of NP treatment and geo-cytotype (Table 1). In general, plants produced significantly more clonal ramets with increasing NP (clonal ramet LSMeans $\pm$ 1 SE under low NP = 6.70 $\pm$ 0.45, medium NP = 11.66 $\pm$ 0.45, high NP = 14.19 $\pm$ 0.45). Furthermore, regardless of NP treatment, diploids and native tetraploids both produced, on average, significantly more ramets than hexaploids;

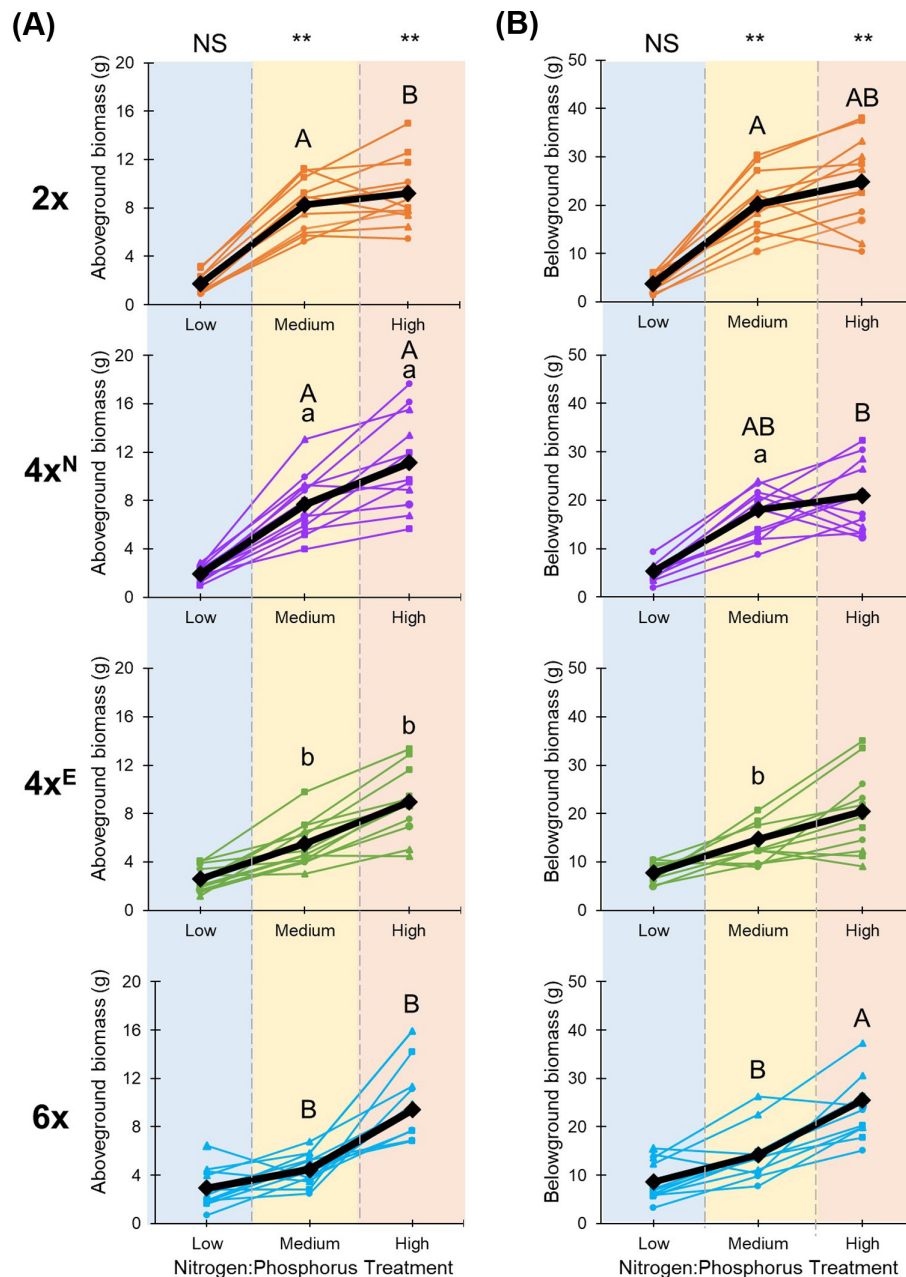


Figure 1. Reaction norm plots depicting phenotypic plasticity for aboveground biomass (A) and belowground biomass (B) for different maternal lines (colored lines with shapes representing a maternal line within a cytotyp) within diploid (2x), North American tetraploid (4x^N), European tetraploid (4x^E), and hexaploid (6x) *Solidago gigantea* populations. The black symbols and lines represent the Least square (LS) mean values and LS mean phenotypic plasticity reaction norm slopes, respectively, for a geo-cytotype. The results of controlled contrasts between native cytotypes and regional tetraploids within the low (blue), medium (yellow), and high (red) nitrogen:phosphorus treatments are depicted with uppercase and lowercase letters, respectively. Full statistical details and controlled contrasts for mean and phenotypic plasticity (PP) values can be found in Table 1–4.

and, among regional tetraploids, North American tetraploids produced, on average, significantly more ramets than European tetraploids (Table 2, Fig. 3A). Clonal ramet PP responses significantly varied among geo-cytotypes dependent upon changes in nutrients, although no other factors significantly affected clonal ramet PP responses (Table 3, see the Supporting information for reaction norm plot).

Specifically, while native cytotypes showed no differences in PP responses, regardless of shifts in the nutrient environment, North American tetraploids were significantly more plastic and produced relatively more ramets than European tetraploids when nutrients shifted from low to medium but not when nutrients shifted from medium to high (Table 4, Fig. 3B).

Table 3. Results of fixed-effects ANOVA models for phenotypic plasticity (PP) values testing whether geo-cytotype (diploid=2x, North American tetraploids=4x^N, European tetraploids=4x^E, hexaploid=6x), soil nutrient level change (low-medium, medium-high), their interaction, and/or geo-cytotype nested within population of origin affected growth traits, clonal ramet production, physiological traits, and resistance traits. Overall model results are reported in the footnotes and bold values indicate a significant effect at $\alpha=0.05$.

Independent factors	df	MS	F	Prob > F
Aboveground biomass				
Geo-cytotype (C)	3	8.93	2.22	0.0918
Nutrient level change (NL)	1	13.11	3.27	0.0746
C × NL	3	67.79	16.89	< 0.0001
Population [C]	7	6.02	1.50	0.1798
Model error	79	4.01		
Belowground biomass				
Geo-cytotype (C)	3	73.62	2.52	0.0642
Nutrient level change (NL)	1	119.70	4.09	0.0465
C × NL	3	254.06	8.71	< 0.0001
Population [C]	7	29.36	1.00	0.4352
Model error	79	29.25		
R:S ratio				
Geo-cytotype (C)	3	0.03	0.14	0.9373
Nutrient level change (NL)	1	0.18	0.95	0.3329
C × NL	3	0.01	0.07	0.9746
Population [C]	7	0.11	0.58	0.7712
Model error	79	0.19		
Clonal ramets				
Geo-cytotype (C)	3	9.31	0.90	0.4436
Nutrient level change (NL)	1	18.61	1.80	0.1830
C × NL	3	40.56	3.93	0.0114
Population [C]	7	14.84	1.44	0.2016
Model error	79	10.31		
A_{max}				
Geo-cytotype (C)	3	8.08	1.66	0.1826
Nutrient level change (NL)	1	5.67	1.16	0.2840
C × NL	3	7.24	1.49	0.2246
Population [C]	7	2.92	0.60	0.7536
Model error	79	4.87		
WUE_i				
Geo-cytotype (C)	3	0.14	7.07	0.0003
Nutrient level change (NL)	1	0.03	1.78	0.1856
C × NL	3	0.01	0.56	0.6408
Population [C]	7	0.01	0.46	0.8636
Model error	79	0.02		
Leaf insect resistance				
Geo-cytotype (C)	3	0.02	2.00	0.1202
Nutrient level change (NL)	1	0.00	0.48	0.4916
C × NL	3	0.00	0.40	0.7562
Population [C]	7	0.07	3.30	0.0040
Model error	79	0.00		
Leaf pathogen resistance				
Geo-cytotype (C)	3	0.01	0.39	0.7591
Nutrient level change (NL)	1	0.02	0.98	0.3261
C × NL	3	0.07	1.11	0.3483
Population [C]	7	0.27	1.89	0.0815
Model error	79	0.02		

Overall model results for aboveground biomass: $R^2=0.47$, $F_{14,93}=5.07$, $p < 0.0001$, $n=94$; belowground biomass: $R^2=0.36$, $F_{14,93}=3.24$, $p=0.0004$, $n=94$; R:S ratio: $R^2=0.07$, $F_{14,93}=0.40$, $p=0.9704$, $n=94$; clonal ramets: $R^2=0.26$, $F_{14,93}=1.96$, $p=0.0322$, $n=94$; A_{max} : $R^2=0.16$, $F_{14,93}=1.10$, $p=0.3702$, $n=94$; WUE_i : $R^2=0.26$, $F_{14,93}=2.00$, $p=0.0285$, $n=94$; leaf insect resistance: $R^2=0.25$, $F_{14,93}=1.92$, $p=0.0358$, $n=94$; leaf pathogen resistance: $R^2=0.19$, $F_{14,93}=1.32$, $p=0.2132$, $n=94$.

Physiological traits

Population of origin, geo-cytotype, and NP treatment each significantly and affected mean maximum photosynthetic

capacity (A_{max}), but differences among geo-cytotypes did not depend upon NP treatment (Table 5). Among native cytotypes, mean A_{max} values significantly increased with ploidy level, and no significant differences were detected between

Table 4. Results of controlled contrast post hoc tests for significant model factors 'geo-cytotype $\times$ nutrient treatment' and 'geo-cytotype' for phenotypic plasticity values (Table 3). These controlled contrasts were used to test whether there were significant differences between native cytotypes (diploids (2x), North American tetraploids (4x^N), and hexaploids (6x)), or between regional tetraploids (North American tetraploids (4x^N) and European tetraploids (4x^E)) within or independent of soil nutrient level changes (low-medium, medium-high). Bold values indicate a significant effect at $\alpha=0.05$.

	F _(df1,df2)	Prob > F	t-test results
Within geo-cytotype $\times$ NP level change			
Aboveground biomass			
Low to med for native cytotypes	14.69 _(2,79)	< 0.0001	4x ^N = 2x > 6x
Low to med for regional tetraploids	13.69 _(1,79)	0.0004	4x ^N > 4x ^E
Med to high for native cytotypes	8.42 _(2,79)	0.0005	6x > 4x ^N > 2x
Med to high for regional tetraploids	0.01 _(1,79)	0.9175	
Belowground biomass			
Low to med for native cytotypes	14.34 _(2,79)	< 0.0001	2x > 4x ^N > 6x
Low to med for regional tetraploids	5.91 _(1,79)	0.0173	4x ^N > 4x ^E
Med to high for native cytotypes	3.28 _(2,79)	0.0429	6x > 4x ^N = 2x
Med to high for regional tetraploids	0.03 _(1,79)	0.8727	
Clonal ramets			
Low to med for native cytotypes	2.81 _(2,79)	0.0660	
Low to med for regional tetraploids	5.86 _(1,79)	0.0178	4x ^N > 4x ^E
Med to high for native cytotypes	2.60 _(2,79)	0.0804	
Med to high for regional tetraploids	0.01 _(1,79)	0.9117	
Within geo-cytotype			
WUE_i			
Native cytotypes	10.09 _(2,79)	0.0001	4x ^N > 2x = 6x
Regional tetraploids	9.49 _(1,79)	0.0028	4x ^N > 4x ^E

North American and European tetraploids ($A_{\max}$ LSMeans $\pm$ 1 SE for 2x = 8.95 ± 0.37 , 4x^N = 10.58 ± 0.37 , 4x^E = 11.56 ± 0.39 , 6x = 12.97 ± 0.39 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Table 2). Plants grown in medium- and high-NP treatments also had significantly greater $A_{\max}$ values than those grown in low-NP treatments ($A_{\max}$ LSMeans $\pm$ 1 SE under low NP = 10.66 ± 0.32 , medium NP = 12.22 ± 0.32 , high NP = 10.18 ± 0.32 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Table 2). No model factors nor interactions among model factors influenced $A_{\max}$ plasticity responses (Table 3).

Geo-cytotypes and plants grown in different NP treatments significantly differed in mean instantaneous water use efficiency (WUE_i) values, although differences did not depend upon each other nor on population of origin (Table 5). Plants grown in high-NP treatments were significantly the most water use efficient (WUE_i LSMeans $\pm$ 1 SE under low NP = 0.33 ± 0.02 , medium NP = 0.39 ± 0.02 , high NP = 0.47 ± 0.02 $\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$). Specifically, native tetraploids and hexaploids were significantly more efficient at using water than diploids (larger WUE_i values), and North American tetraploids were significantly more water use efficient than European tetraploids regardless of NP treatment (Table 2, Fig. 4A). In contrast, geo-cytotype, but no other model factors, significantly affected WUE_i PP responses (Table 3, Supporting information for reaction norm plot) with native tetraploids having greater WUE_i plasticity than all the other geo-cytotypes (Table 4, Fig. 4B).

Resistance traits

No model factors nor interaction among factors significantly affected resistance to insect damage (Table 5) although PP

for resistance to insect damage significantly differed among populations (Table 3). In contrast, plants of different geo-cytotypes and populations of origin significantly differed in resistance to leaf pathogen damage (Table 5). Among native cytotypes, hexaploids were significantly the most, tetraploids intermediate, and diploids the least resistant to pathogen damage, while no significant differences in mean resistance to pathogen damage were found between regional tetraploids (pathogen resistance LSMeans $\pm$ 1 SE for 2x = 0.32 ± 0.02 , 4x^N = 0.42 ± 0.02 , 4x^E = 0.39 ± 0.02 , 6x = 0.55 ± 0.02 ; Table 2). We found neither model factors nor interactions among model factors to have a significant effect on PP in resistance to pathogen damage (Table 3).

Discussion

Changes in local abiotic and biotic environments from anthropogenic activities, such as urban and agricultural development, can selectively favor some species and/or populations within a species over others and influence the likelihood of invasive species success (MacDougall et al. 2013, González-Moreno et al. 2015, Hulme 2017). Polyploidy and high levels of PP have jointly been hypothesized to contribute to invasive successes (Hahn et al. 2012, Sánchez Vilas and Pannell 2017, Wei et al. 2019, Harms et al. 2021), although we generally lack sufficient data for a thorough consensus. Here, we examined whether polyploidy in *S. gigantea* (in which tetraploid cytotypes are invasive; Schlaepfer et al. 2008, 2010) is associated with traits and increased plasticity responses that might have conferred invasive success of tetraploid cytotypes in novel ranges characterized by nutrient enrichments. We

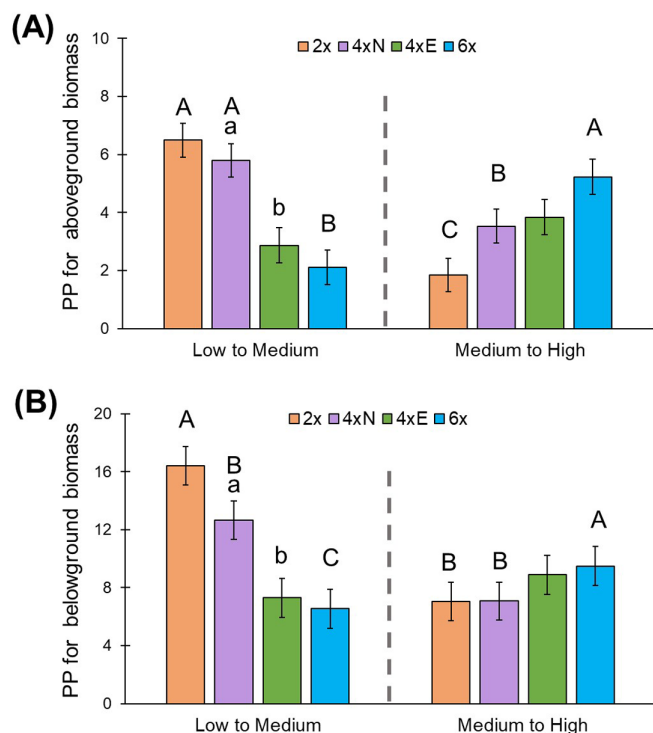


Figure 2. Least square mean aboveground phenotypic plasticity (PP) values (A) and belowground PP values (B) for diploid (2x), North American tetraploid (4x^N), European tetraploid (4x^E), and hexaploid (6x) *S. gigantea* populations as the nutrient environment shifted from low to medium and from medium to high. Shifts in the nutrient environment and geo-cytotype had a significant, interacting effect on above- and belowground PP (model interaction of geo-cytotype $\times$ nutrient level change for aboveground biomass PP: $F_{3,79} = 16.89$, $p < 0.0001$; for belowground biomass PP: $F_{3,79} = 8.71$, $p < 0.0001$). Significant differences in both above- and belowground PP were found between native cytotypes (2x, 4x^N, 6x; denoted by uppercase letters) and regional tetraploids (4x^N, 4x^E; denoted by lowercase letters) from low to medium NP shifts, and only native cytotypes differed in aboveground PP within medium to high NP shifts (denoted by uppercase letters). Error bars represent ± 1 standard error. Full statistical details and controlled contrasts are reported in Table 3 and 4, respectively.

found that trait means and PP values did not always increase with increasing ploidy level (our main hypotheses), but that trait means and PP values varied among geo-cytotypes, traits, and NP soil conditions. Below we discuss these findings and reference how they may provide insights into *S. gigantea* invasive dynamics and cytotype geographic patterning.

Mean trait values and phenotypic plasticity responses varied among *S. gigantea* cytotypes

Whole genome duplication is thought to increase genomic and transcriptomic content and genetic flexibility (Sémon and Wolfe 2007, Soltis et al. 2015, Ding and Chen 2018, Doyle and Coate 2019), and we therefore expected that trait mean and PP responses would positively scale with ploidy level. For example, several studies have shown that polyploidy

Table 5. Results of fixed-effects ANOVA models for mean values testing whether geo-cytotype (diploid=2x, North American tetraploids=4x^N, European tetraploids=4x^E, hexaploid=6x), soil NP treatments (L=low, M=medium, H=high), their interaction, and/or geo-cytotype nested within population of origin affected growth, physiological, and resistance traits. Overall model results are reported in the footnotes and bold values indicate a significant effect at $\alpha=0.05$.

Independent factors	df	MS	F	Prob > F
R:S ratio				
Geo-cytotype (C)	3	0.70	7.60	< 0.0001
NP treatment (NP)	2	0.32	3.49	0.0318
C $\times$ NP	6	0.24	2.60	0.0182
Population [C]	8	0.19	2.07	0.0388
Model error	265	0.09		
A_{max}				
Geo-cytotype (C)	3	204.90	20.99	< 0.0001
NP treatment (NP)	2	108.35	11.10	< 0.0001
C $\times$ NP	6	8.42	0.86	0.5231
Population [C]	8	28.70	2.94	0.0036
Model error	267	9.76		
WUE_i				
Geo-cytotype (C)	3	0.50	12.26	< 0.0001
NP treatment (NP)	2	0.49	11.98	< 0.0001
C $\times$ NP	6	0.05	1.25	0.2803
Population [C]	8	0.06	1.43	0.1834
Model error	267	0.04		
Leaf insect resistance				
Geo-cytotype (C)	3	0.01	2.01	0.1133
NP treatment (NP)	2	0.01	1.81	0.1660
C $\times$ NP	6	0.00	0.30	0.9348
Population [C]	8	0.01	0.92	0.5020
Model error	267	0.00		
Leaf pathogen resistance				
Geo-cytotype (C)	3	0.68	19.53	< 0.0001
NP treatment (NP)	2	0.10	2.81	0.0619
C $\times$ NP	6	0.04	1.15	0.3316
Population [C]	8	0.19	5.49	< 0.0001
Model error	267	0.03		

Overall model for: R:S ratio: $R^2=0.19$, $F_{19,265}=3.42$, $p < 0.0001$, $n=285$; A_{max}: $R^2=0.30$, $F_{19,286}=5.99$, $p < 0.0001$, $n=287$; WUE_i: $R^2=0.23$, $F_{19,286}=4.09$, $p < 0.0001$, $n=287$; leaf insect resistance: $R^2=0.06$, $F_{19,286}=1.00$, $p=0.4661$, $n=287$; leaf pathogen resistance: $R^2=0.30$, $F_{19,286}=5.92$, $p < 0.0001$, $n=287$.

results in the duplication of defense genes and that polyploids may experience less damage by pathogens and herbivores (Nuismer and Thompson 2001, Hannweg et al. 2016, Hias et al. 2018). Similarly, studies with *S. gigantea* have found that tetraploids tend to exhibit phenotypes intermediate of diploids and hexaploids for some traits such as abaxial leaf pubescence and height (Nagy et al. 2018, Martino et al. 2020) but not others, such as leaf length and width (Martino et al. 2020). Here we found support for tetraploid intermediacy for some traits such as photosynthetic capacities, water use efficiencies, and leaf pathogen resistance. However, patterns for many other trait means did not scale positively with ploidy level, but instead varied among traits and nutrient conditions. For instance, tetraploids produced the most clonal ramets, and hexaploids were on average smaller in their aboveground biomass than diploids, which

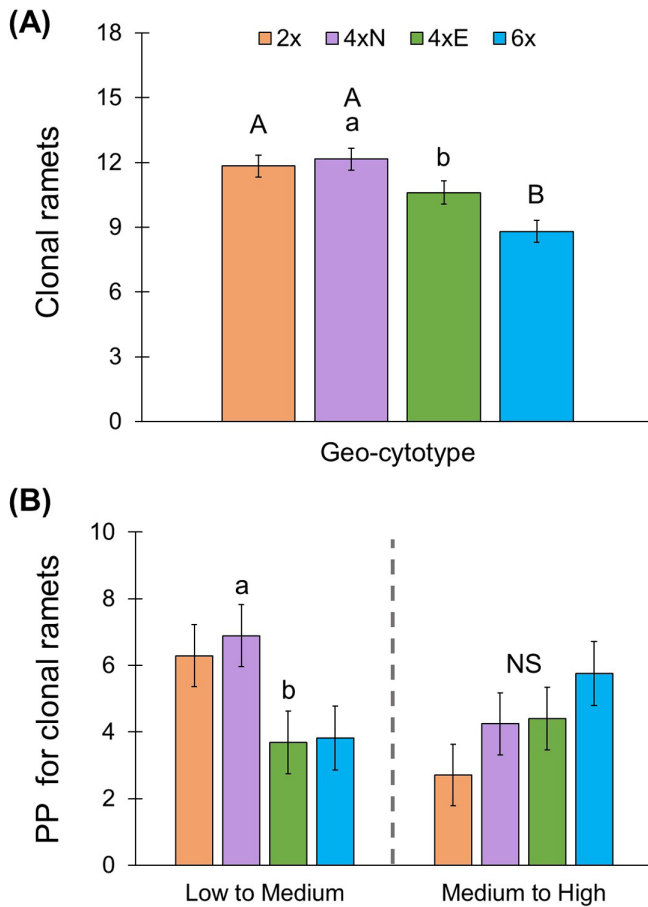


Figure 3. Differences in clonal ramet (A) mean values between geo-cytotypes ($F_{3,267} = 8.18$, $p < 0.0001$) regardless of nitrogen and phosphorus (NP) treatment and (B) phenotypic plasticity (PP) values between geo-cytotypes as the nutrient environment shifted from low to medium and from medium to high (model interaction of geo-cytotype $\times$ nutrient level change for clonal ramet PP: $F_{3,79} = 3.93$, $p = 0.0114$). Significant differences were found between native cytotypes (2x, 4x^N, 6x; denoted by uppercase letters) and regional tetraploids (4x^N, 4x^E; denoted by lowercase letters) for both mean values (both native cytotypes and regional tetraploids) and for when the NP environment shifted from low to medium (regional tetraploids only). Error bars represent ± 1 standard error. Full statistical details and controlled contrasts for mean and PP values can be found in Table 1–4. Reaction norm plots can be found in the Supporting information.

were smaller than tetraploids, but only under medium- and high-NP conditions. Furthermore, while we generally did not detect many differences in plasticity patterns, significant differences included PP responses that both increased and decreased with ploidy level dependent upon trait and/or soil NP shift. For example, although biomasses increased under nutrient enrichments, biomass plasticity tended to decrease with ploidy level in low- to medium-NP shifts but increased with ploidy level in medium- to high-NP shifts. This finding is especially interesting because it indicates that polyploids might be more growth constrained by nutrient limitations than diploids and are 'released' from nutrient constraints

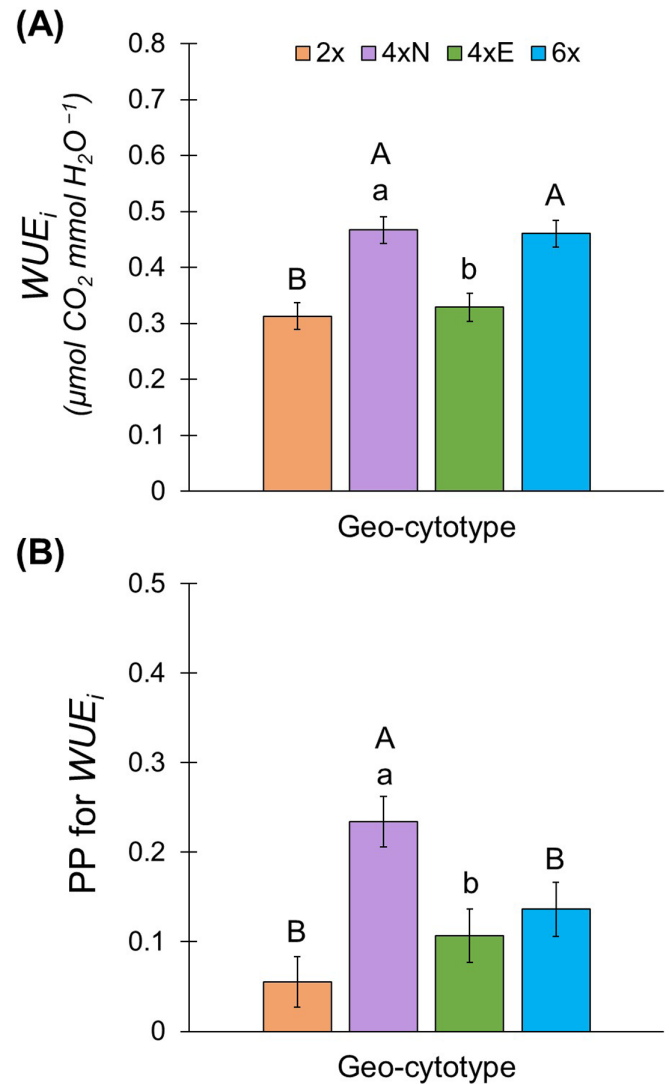


Figure 4. Differences between geo-cytotypes in instantaneous water use efficiency (WUE_i , A) mean values ($F_{3,267} = 12.26$, $p < 0.0001$) and (B) phenotypic plasticity (PP) values ($F_{3,42} = 7.07$, $p = 0.0125$). Significant differences in WUE_i mean and PP values were found between both native cytotypes (2x, 4x^N, 6x; denoted by uppercase letters) and regional tetraploids (4x^N, 4x^E; denoted by lowercase letters). Error bars represent ± 1 standard error. Full statistical details and controlled contrasts for mean and PP values can be found in Table 1–4. Reaction norm plots can be found in the Supporting information.

under soil enrichment. This is congruent with recent studies from a diversity of plant species showing that plants with larger genome sizes and/or polyploids grow more or have higher fitness increases than plants with smaller genome sizes and/or diploids following nutrient additions (Hessen et al. 2013, Neiman et al. 2013, Šmarda et al. 2013, Guignard et al. 2016, Bales and Hersch-Green 2019, Walczyk and Hersch-Green 2019, 2022, Anneberg and Segraves 2020, Peng et al. 2022). Studies using different environmental conditions, traits, and species have also found that PP responses of polyploids versus diploids are variable, with polyploids sometimes

being more (Hahn et al. 2012, Rejlová et al. 2019) and less plastic (Wei et al. 2019, Harms et al. 2021).

Pre-adaptive attributes of tetraploids may have contributed to their invasive success

Research efforts have attempted to identify organismal traits that enhance invasion success and/or allow for rapid adaptation to novel, non-native habitats (Van Kleunen et al. 2010, Matzek 2012). *Solidago gigantea* is a broadly distributed polyploid complex in North America, but only tetraploids are noxious invaders in Eurasia (Schlaepfer et al. 2008, 2010). Similar patterns in which a polyploid cytotype is more invasive than related diploids (their presumed progenitors) have been documented in at least sixteen other polyploid systems (Te Beest et al. 2012), suggesting that certain traits associated with polyploidy and/or the invasive cytotype may innately predispose them to be better invaders. Within *S. gigantea*, diploid and tetraploid cytotypes are more likely than hexaploid cytotypes to have been introduced into Europe during the 1700s and 1800s, based on their current range distributions and where people were settled during that time (Weber and Schmid 1998, Weber and Jakobs 2005). Therefore, we primarily compare diploids to native tetraploids to assess whether innate trait mean and/or PP responses of tetraploids may have favored their success over diploids.

Tetraploids expressed higher trait mean values and PP responses than diploids for several traits that are expected to promote invasive success. For example, regardless of soil NP conditions, tetraploids were more resistant to fungal leaf pathogen damage, exhibited higher water use efficiencies and photosynthetic capacities, and were more PP in their adjustment of water use efficiency responses to shifts in soil NP; all of these traits might allow them to better tolerate and grow in novel and/or heterogeneous environments with unfamiliar pathogens, nutrients, and water availabilities (Pigliucci et al. 2006, Richards et al. 2006, Van Kleunen et al. 2010, Gratani 2014, Colautti et al. 2017). Furthermore, under low soil NP conditions tetraploids invested more into roots than shoots relative to diploids, but under high soil NP conditions they invested less into roots than shoots relative to diploids (patterns which are also reflected by differences in biomass PP responses). Higher investment into belowground relative to aboveground biomass under low soil NP conditions may increase tetraploid tolerance or competition for belowground resources under nutrient limitations (Gioria and Osborne 2014, Goldberg et al. 2017), whereas the ability to invest more into aboveground biomass when nutrients become less limiting may make them more competitive over diploids when light and space become limited (Wilsey and Polley 2006, Heberling and Fridley 2013). Competitive advantages associated with increased above- or belowground biomass investments are well-documented in other invasive plant species (e.g. *Solidago canadensis*, Huang et al. 2007; *Alternanthera philoxeroides*, You et al. 2016; *Elodea nuttallii*, *Myriophyllum aquaticum* and *M. propinquum*, Xie et al. 2010), and are suspected to be especially advantageous to

new invaders that are exposed to heterogeneous environments occupied by well-adapted local competitors (You et al. 2016). Therefore, cumulatively we found that native tetraploid *S. gigantea* express traits that may have allowed them to outcompete co-occurring diploids after introduction into novel areas. Furthermore, as we primarily observed tetraploid biomass advantages under nutrient enriched treatments, introduction into urban and agricultural environments that tend to be characterized by super-enriched conditions (Broadbent et al. 2018, Akin-Fajiyi et al. 2021) may have also contributed to the early success of *S. gigantea* tetraploids. However, it is difficult to determine whether the invasion success of these tetraploids is due to their competitive superiority in novel (and potentially nutrient enriched) environments and/or to serendipitous events, such as tetraploids being the only cytotype introduced.

Little evidence for post-introduction selection

While the success of biological invasion may partly be due to traits and/or strategies already present in the invading genotypes (Van Kleunen et al. 2011, Oh et al. 2021, Kaushik et al. 2022), post-invasion selection pressures could also influence fitness, competitive, and tolerance traits (Zenni et al. 2014, Elst et al. 2016, Stutz et al. 2018) and thus the long-term persistence of genotypes in novel environments. Therefore, we also explored whether post-introduction selection may have led to different mean trait values and PP responses within populations of native- and non-native *S. gigantea* tetraploids.

Native North American and non-native European tetraploids tended to differ from each other in some traits that should confer success in competition and persistence in novel environments, but in all cases where we detected differences, native tetraploids had higher values (e.g. larger biomass, greater ramet production, more water use efficient, and more PP in biomass accumulation, clonal ramet production, and water use efficiency). Our results contrast other findings, which have found that *S. gigantea* genotypes from non-native populations outperformed genotypes from native populations in terms of height, clonal ramet production, and biomass production (Nagy et al. 2018) and compensation to insect damage (Liao et al. 2016). Inconsistency among these comparisons of native and non-native *S. gigantea* among studies and the fact that the native tetraploids in our experiments outperformed the non-native tetraploids could be due to many factors. For instance, unique genotypes collected from different populations may be locally adapted to specific conditions and thus express traits differently when grown in the presence of native versus non-native climates, soils, symbiotes, and/or antagonists (Pal et al. 2020, Sheng et al. 2022). In our study, we do not know the North American source populations from which the non-native tetraploids originated and thus it is impossible to definitively extrapolate. Furthermore, sampling biases and genetic drift may have contributed to our results. For example, in our study we collected native tetraploids that were well distributed across their native range (Supporting information), which could either

underestimate total cytotype trait variability due to locally adapted genotypes (Rosche et al. 2019) and/or inflate native cytotype trait variability relative to the non-native cytotypes (collection range was limited due to logistical constraints). Furthermore, it is likely that our non-native tetraploid populations experienced genetic drift via founder effects, since all our non-native tetraploids populations originated from urban areas around Zürich, Switzerland (Supporting information). Sampling bias and concurrent genetic drift processes are typical of invasions (Lee 2002, Bélouard et al. 2019) and can result in the fixation of those traits at specific values independent of trait-associated fitness effects (Tsutsui et al. 2000) and may also constrain trait plasticity, as PP has been shown to correlate with genetic variation (Noble et al. 2019, Landy et al. 2020). Lastly, selective processes may have contributed but there may not have been enough evolutionary time for native and non-native populations to diverge in their trait expression; and/or selection pressures on invasive genotypes and traits might vary across environments and stages of biological invasion. For instance, plasticity differences might be most visible early in an invasion, before adaptation can occur (Palacio-López and Gianoli 2011), and PP might not be beneficial under all conditions as it can be costly to execute and maintain (Wolfe and Mazer 2005, Auld et al. 2010, Murren et al. 2015).

Conclusion

Biological invasions represent a global ecological and economic threat (Ehrenfeld 2010, Diagne et al. 2021) and understanding the species traits and/or environmental conditions that render some genotypes being more successful than others is an important step in minimizing and controlling their impacts. We sought to examine the degree to which ploidy variation and environmental NP enrichment (both conditions commonly cited as being relevant to biological invasions; Pandit et al. 2011, Te Beest et al. 2012, Broadbent et al. 2018, Akin-Fajiye et al. 2021, Moura et al. 2021, Rutland et al. 2021) affect trait expression and plasticity responses of native and non-native cytotypes of *S. gigantea*. In general, we found little evidence to suggest that polyploidy and/or post-introduction selection processes shaped PP responses, although tetraploids did possess traits and PP responses that were indicative of superior competitive abilities, persistence in variable environments, and responsiveness to nutrient enrichment relative to diploids. Future studies should continue to address these questions in a range of invasive and native genotypes in different environments, to better tease apart whether and at what stage in the invasion process increased PP and/or higher trait values might confer the greatest fitness advantages.

Speculations

In our experiment, we found that polyploids sometimes increased trait means and/or PP responses as NP availability

increased, but this was primarily limited to biomass traits. While our results did not provide enough evidence for us to conclude that nutrient enrichment conveys a competitive and fitness advantage in polyploids over diploids, we speculate that traits inherent to tetraploids and high levels of plant available nutrients played a joint role in *S. gigantea*'s success as an invasive species. Because N and P availability is increasing in terrestrial and aquatic ecosystems globally (Penuelas et al. 2013, Fowler et al. 2015, Goyette et al. 2016, Asabere et al. 2018), we also speculate that ecosystems characterized by intense nutrient eutrophication may have been or might become especially prone to polyploid biological invasions (Luo et al. 2019).

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Author contributions

Angela M. Walczyk: Conceptualization (equal); Formal analysis (equal); Funding acquisition (supporting); Writing – original draft (equal); Writing – review and editing (equal).
Erika I. Hersch-Green: Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3j9kd51qs> (Walczyk and Hersch-Green 2023).

Supporting information

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

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