**Polyploidy mediates loss of plasticity during domestication in tuber-bearing *Solanum* section *Petota***

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**Abstract**

Phenotypic plasticity may be an important component of plant fitness and survival in the face of environmental variation. However, adaptive plasticity may be subject to loss in stable environments where changes leading to selection for plasticity are rare and genetic drift and selection can result in the loss of genetic variation underlying plasticity. During domestication and cultivation growers strive, though agricultural practices, to reduce environmental variation and this may contribute to a loss of phenotypic plasticity. Polyploidy, possessing more than two complete sets of chromosomes, reduces the effect of drift by increasing the gametic heterozygosity of a population. Reduced drift may slow the loss of plasticity in polyploid crops compared to diploids. Here, we investigate whether polyploidy has contributed to differences in phenotypic plasticity in wild and landrace potato populations of *Solanum* section *Petota*. We compare expressed plasticity in experimentally controlled nitrogen treatments between diploid and polyploid, landrace and wild populations of section *Petota*. We test whether domestication has diminished plastic response and whether polyploidy maintains plastic response in the face of domestication. We find no consistent difference in plasticity between wild diploid and tetraploid populations, but landrace diploid populations expressed less plasticity than wild diploid populations. We also find that tetraploid landrace populations expressed greater plasticity than diploid landraces and were more similar to both wild populations. These results suggest that polyploidy *per se* does not confer increased plasticity in response to variation in nitrogen but has limited the loss of plasticity during domestication in potato.

Keywords: phenotypic plasticity, domestication, polyploidy, genotype-by-environment interaction

**Introduction**

Phenotypic plasticity, an organism’s expression of different phenotypes depending on its environment, may be an important component of fitness in the face of spatial and temporal environmental variation (1). Adaptive phenotypic plasticity, plasticity which results in a phenotype closer to the optimal value for an environment, is thought to be especially important for plants due to their sessile lifestyle, such that individuals are subject to whatever environment they grow in (2). This may be exaggerated in perennial plant species whose individuals face both intra- and inter-seasonal environmental variation (3). Plasticity varies both within and between populations and species (4), at least partially, due to genetic variation (5). Heritable variation in plasticity can lead to variation in fitness and, thus, selection for plastic response to certain environments (4,6–8). Phenotypic plasticity is generally understood to be a highly polygenic trait, influenced by many loci of small effect dispersed across the genome, many of which may continue to segregate even in the face of selection for increased plasticity (9). This suggests that plastic responses to environments rarely experienced by a population may be subject to loss by genetic drift (10–12).

Many studies have found that polyploid species have an expanded range compared to their diploid progenitors, such as in *Solidago canadensis* (13), *Centaurium* (14), and *Solanum* section *Petota* (15). Polyploidy has also generally been considered to contribute to the success of invasive species (16–18). One potential explanation for this suggested in theoretical literature is that polyploids may express higher adaptive phenotypic plasticity, allowing them to maintain higher fitness while they expand into new environments (17–20). Empirical studies in domesticated species show that polyploidy is often associated with increased plasticity, generally discussed in terms of stress response, e.g. (21–25). Many studies in wild species, on the other hand, have found little to no evidence of ploidy-mediated plasticity, e.g. (26–29). Further research is needed to bridge the gap between results seen in domesticated and wild species.

There is ample evidence that diploids tend to lose plasticity for many traits and environments studied as species undergo domestication. For example: plasticity in growth-form was maintained in cassava during domestication, but stem mechanical properties between growth-forms were reduced in domesticated populations (30); circadian rhythm modulation in response to elevated temperatures was reduced in domesticated barley (31); and plastic responses in modern wild sunflower populations were reduced when compared to resurrected, antecedent wild populations for many phenological traits in response to water and temperature treatments, which was suggested to have been caused by gene flow from domesticated populations (32). A potential explanation for the observed loss of plasticity discussed above is genetic drift leading to the alleles underlying plasticity to be lost after selection is reduced in the face of agricultural inputs homogenizing the environment (33,34). Another explanation for a loss in phenotypic plasticity is that the plasticity, in itself, may impose a cost to plant fitness and selection may act to remove it in stable environments (10,33–36). In both cases, the increased gametic heterozygosity in polyploid species would slow the loss of plasticity: the effect of drift is reduced in polyploid populations when compared to diploid populations (37) and response to selection in autotetraploids is half that of diploids (38,39). In reality, the answer probably lies somewhere between these two extremes: selection tends to reduce plasticity in traits when there is a cost to fitness, and plasticity in traits with no fitness cost may decline due to drift when selection favoring plasticity is relaxed.

Observed differences in plasticity between domesticated diploid and polyploid populations, therefore, may be due to an interaction between ploidy and domestication, rather than ploidy *per se*. In wild populations, there may be continual selection for adaptive plasticity irrespective of ploidy. However, while the relationships between plasticity and ploidy (40–46) and plasticity and domestication (30,31,47–49) have been empirically studied, the interaction between these factors in relation to plasticity has not. Indeed, this problem is particularly troublesome to address as it is difficult to disentangle the effect of ploidy and domestication on expressed plasticity from population dynamics and stochasticity within ploidy or improvement status, especially at long enough timescales to see the effects of genomic buffering between factors. Here, we study the effect of the interaction between domestication and ploidy on expressed plasticity in wild and domesticated potato (*Solanum* section *Petota*) by sampling within the section in an attempt to draw conclusions about how these factors have influenced the evolution of plasticity in this system.

When investigating plasticity, it is important to note that organisms do not express a general plasticity, but rather plasticity is expressed on a per trait, per environment basis (50). For example, while an organism may show a large plastic response for height in the face of elevated temperature, that does not necessarily mean the same plant would show a similar height response to daylength or show a plastic response for leaf area in the face of elevated temperature. When testing for differences in plasticity, it is vital to select environments that are likely to commonly vary in the natural setting of the species under investigation. It is also important to note that, for plasticity to be selected in a population, it must increase or maintain fitness and survival. That is to say, variability of certain morphological or physiological characters must confer homeostasis in fitness components for it to provide a selective advantage (50). Following this, we hypothesize that plastic response for traits indirectly related to fitness, such as plant height and aboveground biomass, will be diminished in diploid domesticated populations compared to diploid wild, polyploid domesticated, and polyploid wild populations (hereafter, referred to as ‘groups’). We further hypothesize that traits closely related to fitness, such as time to maturity and the number of stolons resulting in a daughter plant or tuber (measures of clonal fitness), will be more responsive to the treatment in diploid domesticated populations when compared to the other three groups.

In this study we investigated the interaction between domestication and ploidy in their effects on the expression of phenotypic plasticity in tuber-bearing *Solanum* section *Petota*, which contains domesticated potato and its wild relatives. Ploidy varies both within and between species in section *Petota*, mainly consisting of diploid and autotetraploid cytotypes, though triploids, pentaploids, and hexaploids also occur naturally (51). Domesticated potato contains four species (*S. tuberosum, S. anjanhuiri, S. juzepezukii, and S. curtilobum*). *S*. *tuberosum*, consists of two major groups (Andigenum Group containing diploids, triploids and tetraploids, and Chilotanum Group consisting entirely of tetraploids) (52). Domestication in *S*. *tuberosum* took place circa 6000 BCE in the Andean highlands of modern Peru and Bolivia based on archeological and molecular evidence (53). While commercial potato varieties in the US and Europe all belong to the autotetraploid *S*. *tuberosum* group Chilotanum, cultivated potato in South America continues to include all four species and varies by ploidy. There are 107 wild species in section *Petota* (e.g., *S*. *brevicaule*, *S*. *chacoense*, *S*. *kurtzianum*, *S*. *medians*, and *S*. *berthaultii*) (54). Wild species naturally range from Argentina and Peru, up through Central America, and into Mexico and the southwestern USA (15,55).

Nitrogen availability has an effect on myriad traits in modern potato cultivars. In general, increased soil nitrogen slows maturity in potato (56–61). While yield is positively correlated with applied nitrogen, this is generally due to an increase in the average mass of individual tubers while the total number of tubers remains constant (58,62). Aboveground biomass is generally greater when nitrogen is plentiful, caused, at least in part, by changes in resource allocation from shoots to roots: plants tend to produce fewer stems with smaller leaves and more roots under low nitrogen treatments (61,63–65). However, even within US and European cultivated potato there is variance in nitrogen response across cultivars and a strong genotype-by-environment interaction effect, indicating variation in plasticity (58,66,67). The broad response of potato to variation in nitrogen availability and the variation in that response makes experimentally controlled nitrogen treatments a good choice for investigating whether polyploidy has played a role in the loss of expressed plasticity in section *Petota*. Furthermore, N availability is likely to differ between wild and cultivated settings, soil fertility has been supplemented by farmers throughout the history of potato cultivation through practices such as guano application, crop rotation, and natural fallowing (51,68). This may have reduced selection for a plastic response to low nitrogen availability.

To assess whether domestication and ploidy interact to influence expression of phenotypic plasticity in *Solanum* section *Petota*, we sampled species across the section and measured expressed plasticity between experimentally manipulated environments. Although it is difficult to disentangle the effects of population-specific dynamics and stochastic processes when comparing long-diverged populations, we attempt to minimize these sources of uncertainty by sampling a factorial combination of improvement status and ploidy from several species and groups/populations within those species. By using this wide sampling strategy, we attempt to draw broad conclusions about the evolution of phenotypic plasticity in tuber-bearing *Solanum*. Specifically, we sought to answer the following questions: (1) Does polyploidy confer increased plasticity in response to nitrogen availability in wild potato populations? (2) Does this expressed phenotypic plasticity diminish during domestication in diploids? And (3) has polyploidy contributed to the maintenance of plastic responses to applied nitrogen during domestication?

**Materials and Methods**

***Seed source***

To minimize the influence of within-species dynamics and stochastic differences between populations within *Solanum* section *Petota*, we chose accessions from several species and subgroups within each ploidy × improvement status group (diploid wild, diploid landrace, tetraploid wild, and tetraploid landrace). We sampled four accessions from each group (16 accessions total) from five species within section *Petota* (*S. brevicaule, S. chacoense, S. kurtzianum, S. medians,* and *S. tuberosum*, Table 1). The landrace accessions included in this study belong to *S. tuberosum* group Andigenum as group Chilotanum is entirely autotetraploid. We sourced all seed from the United States Potato Genebank (USPG, Sturgeon Bay, WI).

Ploidy for all accessions was determined by USPG (US Potato Genebank, npgsweb.ars-grin.gov) by staining the chromosomes in freshly collected root tips and counting them via microscopic observation. Accessions had been collected from sites in Argentina, Bolivia, Chile, Colombia, and Peru from 1951 to 1986 as both seeds and tubers and thereafter maintained by USPG. Accessions’ seed lots are generated by USPG every ~25 years (depending on germination rates during storage) by growing 20 plants from an accession, bulking pollen from all plants, intermating, and bulking the subsequent seed (John Bamberg, personal communications). We are, therefore, unable to make precise determinations about the relatedness of individuals within each accession. This practice has maintained genetic diversity in the accessions when compared to newly collected material (69), so we do not expect that length of time since collection has influenced the expressed plasticity in these accessions.

***Field Year 2022***

We ordered seed of the 16 accessions from the USPG in October 2021. Seed was soaked in a 2000 ppm gibberellic acid solution for 48 hours, germinated on filter paper, and transplanted into the greenhouse in February 2022. Due to low germination rates, only 10 accessions were transplanted into the greenhouse. In May 2022, we cloned each plantlet by stem cutting. Stem cuttings were then allowed to establish and acclimate to greenhouse conditions for 4 weeks, when we randomly selected up to 15 individuals from each accession with at least 6 surviving clones to move forward, resulting in 132 unique individuals (Table 1).

We transplanted the resulting 132 individuals into three urea treatments (0, 172, and 224 kg/ha) with two replicates (6 clones per genotype, 792 plants total) at the Sand Plains Research Farm in Becker, MN on June 8, 2022. Soil at the Sand Plains Research Farm consists of a high percentage of sand and relatively little clay and silt (websoilsurvey.sc.egov.usda.gov). In-row and between-row spacing was 0.9 m. The field was irrigated twice a week throughout the season to maintain well-watered conditions. Pre-emergent herbicide was applied on May 5 and fungicide and pesticides were applied weekly throughout the season (Table S1).

***Field Year 2023***

We received seed from the USPG in March 2023. Due to low germination rates in 2022, we coated seeds in 1% w/v activated charcoal solution following 48-hour gibberellic acid treatment (Bamberg et al., 1986), which substantially increased germination rates and reduced time to germination. Seedlings were transplanted into a growth chamber set to 20ºC on April 12, 2023, and allowed to establish. After 4 weeks, up to 20 individuals, depending on germination rate and plantlet survival, across all 16 accessions were randomly selected to move forward, resulting in a total of 288 unique genotypes. As seed was unavailable when initially requested, we were unable to clone individuals in 2023 due to time constraints.

We transplanted up to 10 individuals per accession (Table 1) into each of the two urea treatments (0 and 172 kg/ha) in a split-plot design on May 19 on the Saint Paul campus at the University of Minnesota. Soil in this location contained a higher percentage of silt and clay and a lower percentage of sand than field year 2022 (websoilsurvey.sc.egov.usda.gov). In-row and between-row spacing was 0.9 m. Plants were irrigated twice a week to maintain well-watered conditions throughout the season. Herbicides, fungicides, and pesticides were not applied to the field in 2023, which resulted in increased weed pressure, though we did not see any increase in pest or fungi pressure.

***Phenotyping***

We collected data on flowering time (FT) as the number of days from transplanting to the first open flower on plant collected every 2-3 days throughout the growing season; plant height (PH) as the height in cm from the base of a plant to its highest point; aboveground biomass (AGB) as the mass in grams of all vines at harvest after drying at 60ºC until mass stabilized. The season in 2022 was cut short leading to PH being taken at harvest (77 days after planting). In 2023, PH was taken 100 days after planting, when all plants had reached full maturity. The number of daughter plants was calculated by the number of visible stems arising from a stolon at least 10 cm from the base of the mother plant at harvest. However, landrace populations have been bred to favor tuber production over daughter plants, and many landrace accessions did not form any daughter plants, making a comparison between landrace and wild accessions meaningless. To account for this in 2023, we also collected tuber count as the total number of developed tubers at harvest and calculated a composite measurement of asexual fitness by adding the number of daughter plants and tuber count to give the number of productive stolons (PS). Tuber count data was not taken in 2022, so we were unable to calculate PS in 2022.

***Statistical Analysis***

All statistical analyses were performed in R v4.3.1 (70) using the *tidyverse* suite of packages (71). We tested for differences in plasticity by ANOVA, testing for differences in trait values for groups in treatment-pairs: (eqn. 1), where γij is the simple slope of group *i* acrosseach treatment-pair *j* and ϵij is the error of those estimates. Significant differences indicate a difference in the slope of at least two groups. We tested for differences in the slope between groups for each trait and each year separately. We adjusted the p-values for all trait-year pairs by controlling for the false discovery rate (FDR). FDR-adjusted p-values were calculated using the Benjamini-Hochberg method (72) for all trait-year pairs simultaneously. To simplify the analysis and to make fair comparisons between years while reducing the total number of tests performed, we only compared the  0 and 172 kg/ha nitrogen treatments for both years.

To compare relative magnitudes of plasticity between groups, we calculate the percent change of each trait in each group by taking the difference in mean of each group in each environment, dividing by the mean of each group across environments and multiplying by 100%: (eqn. 2), where μij´ is the mean of group *i* in environment *j´* and μij´´ is the mean of group *i* in environment *j´´*.

**Results and Discussion**

***Do ploidy × domestication status pairs express differences in plasticity?***

We found significant differences in the ANOVA model for the slopes of all traits in both years after adjusting for multiple testing, indicating that at least two groups were different from one another (Table 2). This result shows that groups expressed differences in their response to applied soil nitrogen for the traits measured, or, expressed in terms of ANOVA, the trends of at least two groups differed across nitrogen treatments (Figure 1).

***Does polyploidy confer increased plasticity in wild potato populations?***

We find little evidence that polyploidy, in itself, confers increased plasticity in wild potato populations when contrasting diploid and tetraploid populations. For FT, we found that diploid populations were more responsive to the treatment than tetraploids in 2022 (∆z 2x: 4.66%; ∆z 4x: 0.820%) but diploids were more stable across treatments than tetraploids in 2023 (∆z 2x: 3.85%; ∆z 4x: 7.15%). For AGB, diploid populations expressed less plasticity than tetraploids in 2022 (∆z 2x: 21.8%; ∆z 4x: 57.5%) but more plasticity in 2023 was found (∆z 2x: 105%; ∆z 4x: 62.0%). Similarly, for PH we find that tetraploid populations expressed greater plasticity in 2022 (∆z 2x: 1.96%; ∆z 4x: 15.6%) but lesser plasticity in 2023 (∆z 2x: 30.8%; ∆z 4x: 17.1%). For PS in 2023, diploids were more stable across environments (∆z 2x: 12.9%; ∆z 4x: 44.4%) (Figure 2).

Our findings are consistent with literature investigating the effect of polyploidy on expressed plasticity in wild populations. Differences in plasticity between wild diploids and tetraploids were inconsistent between years, providing little evidence that polyploidy, in itself, is responsible for generally increased plasticity. These data support our hypothesis that polyploidy *per se* does not confer increased plasticity to variation in soil nitrogen in wild populations.

***Does expressed phenotypic plasticity diminish during domestication in diploids?***

         Our results suggest that domestication has reduced plasticity to response to nitrogen treatments in diploid potato populations. For FT, diploid landrace populations were more responsive to the nitrogen treatment than diploid wild populations in 2022 (∆z landrace: 8.77%; ∆z wild: 4.66%) and 2023 (∆z landrace: 13.6%; ∆z wild: 3.85%). Diploid landrace populations showed lesser plasticity for AGB both 2022 (∆z landrace: 21.5%; ∆z wild: 21.8%) and 2023  (∆z landrace: 8.72%; ∆z wild: 105%). PH was more responsive in diploid wild populations than diploid landrace populations in 2022 (∆z landrace: 0.150%; ∆z wild: 1.96%) and 2023 (∆z landrace: 5.83%; ∆z wild: 30.8%). In 2023, PS was more responsive in diploid landrace populations than wild populations (∆z landrace: 41.9%; ∆z wild: 12.9%) (Figure 2).

The patterns of differences in ∆z between landrace and wild diploid populations for all traits matched our expectations and provide evidence for our hypothesis that domestication has acted to generally reduce plasticity to applied soil nitrogen for vegetative traits, while maintaining homeostasis in fitness components.

***Has polyploidy acted to maintain plastic responses during domestication?***

To understand whether an interaction between domestication and ploidy have influenced the evolution of plasticity in tuber-bearing *Solanum*, we examined differences in ∆z for diploid and tetraploid landrace populations. Diploid landrace populations were more variable for FT than tetraploids in 2022 (∆z 2x: 8.77%; ∆z 4x: 0.820%) and 2023 (∆z 2x: 13.6%; ∆z 4x: 11.5%). AGB was more plastic in tetraploid landrace populations than diploid landrace populations in both 2022 (∆z 2x: 21.5%; ∆z 4x: 32.3%) and 2023 (∆z 2x: 8.72%; ∆z 4x: 130%). PH in diploid landrace populations was less variable in 2022 (∆z 2x: 0.150%; ∆z 4x: 11.1%) and 2023 (∆z 2x: 5.83%; ∆z 4x: 12.5%). However, PS in 2023 were more variable in tetraploid landrace populations than diploid landrace populations (∆z 2x: 41.9%; ∆z 4x: 77.9%) (Figure 2).

Almost all patterns in ∆z estimates matched our expectations, providing support for our hypothesis that polyploidy acts to maintain plasticity during the domestication process, with the exception of PS. As clonal reproduction is an important part of *Solanum* section *Petota*, we would expect selection to act to increase homeostasis for PS across environments. However, PS was more responsive to the treatment in tetraploid landrace populations compared to diploid landrace populations, indicating that diploid landraces possessed greater homeostasis for PS.

**Conclusions**

To our knowledge, this is the first empirical study to explore the relationship between phenotypic plasticity, polyploidy, and domestication, in part due to the complexity of differentiating the effects of ploidy and domestication on expressed plasticity from random genetic drift and population specific selection pressures. While we attempt to reduce the effects of population dynamics by sampling several populations within each factor pair, this represents only a fraction of the total number of species in section *Petota*. Further, we only tested for plastic response to a single environmental variable and only in a few traits. It is entirely possible that for other environmental gradients which are more likely to vary in the wild than in domesticated settings or for traits not measured here, we would find similar levels of plasticity between these populations, or that diploid landraces may even possess a stronger plastic response. Another caveat present in this study is that most diploid potato species possess S-RNase based self-incompatibility (73), while S-RNase based self-incompatibility has broken down in autopolyploids due to the production of diploid pollen (74). Differences in mating system may influence the genetic diversity between cytotypes and is confounded with ploidy in our study. However, these differences do not appear to substantially have reduced genetic diversity in tetraploid potato species which show similar or even higher levels of heterozygosity than diploids (75,76). While there are certainly caveats with the experiment we presented here, enumerated above, we believe our sampling approach allows us to draw more general conclusions about the evolution of phenotypic plasticity in section *Petota* for the environments and traits tested, and creates a framework for testing the effect of domestication on plasticity in different populations, environments, and traits. We show that, while polyploidy *per se* does not confer increased phenotypic plasticity to variation in nitrogen in wild potato populations, it may act to maintain plasticity during domestication, potentially through an increase in the gametic heterozygosity reducing the effect of drift and selection (37–39,77). This conclusion helps to bridge the divide in the literature between the effects of polyploidy on phenotypic plasticity in domesticated and wild populations. We suggest our results may also explain observations of ploidy-mediated phenotypic plasticity in invasive species, where populations are likely to experience strong selection and the effects of genetic drift are more pronounced due to bottlenecks. An experiment using a similar design but including genomic data to quantify the effects of drift and selection on genomic variants giving rise to plasticity will be an important next step to fully understand the role polyploidy plays in the evolution of phenotypic plasticity during domestication or, potentially, invasion.

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Table 1: List of species and accession numbers, their respective ploidy levels and improvement statuses, as well as the number of unique genotypes included in each field year (N).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  |  |  | **N** | |
| **Species** | **Accession** | **Ploidy** | **Improvement** | **2022** | **2023** | |
| *S. chacoense* | PI 275138 | 2x | Wild | 14 | 12 | |
| *S. brevicaule* | PI 230503 | 2x | Wild | 11 | 20 | |
| *S. kurtzianum* | PI 472944 | 2x | Wild | 14 | 20 | |
| *S. medians* | PI 310994 | 2x | Wild |  | 20 | |
| *S. tuberosum* grp. Andigenum | PI 365344 | 2x | Landrace | 14 | 20 | |
| *S. tuberosum* grp. Andigenum | PI 225677 | 2x | Landrace | 7 | 20 | |
| *S. tuberosum* grp. Andigenum | PI 234011 | 2x | Landrace | 13 | 20 | |
| *S. tuberosum* grp. Andigenum | PI 195198 | 2x | Landrace |  | 16 | |
| *S. brevicaule* | PI 498298 | 4x | Wild | 15 | 20 | |
| *S. chacoense* | PI 498300 | 4x | Wild | 15 | 20 | |
| *S. brevicaule* | PI 458342 | 4x | Wild |  | 20 | |
| *S. brevicaule* | PI 545916 | 4x | Wild |  | 20 | |
| *S. tuberosum* grp. Andigenum | PI 281111 | 4x | Landrace | 14 | 12 | |
| *S. tuberosum* grp. Andigenum | PI 473281 | 4x | Landrace | 15 | 8 | |
| *S. tuberosum* grp. Andigenum | PI 243371 | 4x | Landrace |  | 20 | |
| *S. tuberosum* grp. Andigenum | PI 245320 | 4x | Landrace |  | 20 | |
|  |  |  | Total: | 132 | 288 | |

Table 2: Results of ANOVA for the interaction between group and nitrogen treatment for each trait and year separately.

|  |  |  |
| --- | --- | --- |
| **Year** | **Trait** | **FDR-adjusted *p*** |
| 2022 | Flowering Time | 2.10 × 10-16 |
| 2022 | Aboveground Biomass | 5.63 × 10-19 |
| 2022 | Plant Height | 9.15 × 10-13 |
| 2023 | Flowering Time | 9.97 × 10-7 |
| 2023 | Aboveground Biomass | 5.11 × 10-7 |
| 2023 | Plant Height | 1.10 × 10-7 |
| 2023 | Productive Stolons | 1.95 × 10-6 |

A screenshot of a graph

Description automatically generated

Figure 1: Mean trait values (points) and standard error (vertical lines) for each trait in each treatment, separated by year (A-C: 2022; D-G: 2023). Ploidy-by-domestication status pairs (groups) separated by color. Lines connect mean trait values between treatments.

A screenshot of a graph

Description automatically generated

Figure 2: Change in trait value expressed as a percentage change from one environment to the other (∆z) for each trait, separated by year (A-C: 2022; D-G: 2023). Ploidy-by-domestication status pairs (groups) separated by color.