horticulturae

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Quantifying Intergenerational Plasticity in Tomato: Temporal Divergence as a Cost-Effective Survival Strategy Against Drought Following Parental Ultrasound Priming

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Abstract

Understanding intra- and intergenerational adaptive strategies is essential for developing resilient crops. This study investigated these dynamics in *Solanum lycopersicum* L. cv. Micro-Tom by subjecting parental plants to ultrasound priming and drought stress, followed by drought treatment in the progeny. We introduced the Intergenerational Plasticity Ratio (IPR) as a framework to quantify how stress-response strategies shift across generations. Our results reveal a divergence in adaptation: while parental plants prioritize immediate survival through morphological reductions, the progeny exhibit refined phenological shifts as a cost-effective mechanism. The results suggest that ultrasound may serve as a priming stimulus, preparing internal signaling pathways for heightened stress readiness. These phenotypic shifts suggest that ultrasound-based priming could be explored as a potential non-chemical approach to influence crop resilience. This may allow plants to exhibit adaptive developmental timing in response to specific stressors; however, further research is needed to determine the scalability and stability of these effects across different environments.

Keywords: stress avoidance; intergenerational plasticity ratio; ultrasound priming; Micro-Tom; tomato; epibreeding; Multivariate Plasticity Index

1. Introduction

Climate change impacts vegetables more severely than many other crop types [1]. Because genetic adaptation is potentially too slow to keep up with current climate projections, an organism's capacity for plasticity is its most critical tool for resilience. This ability to flexibly "shape" traits in response to new environmental cues provides a necessary buffer, allowing populations to persist while more permanent genetic solutions are stalled [2]. Ultimately, a species' capability to adjust to a changing environment defines the limits and magnitude of the biological impacts caused by global warming [3].

Phenotypic plasticity—the ability of an organism to alter its phenotype without changing its underlying genetic code—is a cornerstone of adaptation and yield stability in changing environments [4–6]. To secure global food supplies, it is critical to understand how plants leverage this flexibility through strategies like drought priming. By exposing plants to moderate, non-lethal stress, priming triggers a 'stress memory' that expands a genotype's plastic range, enabling more resilient physiological and structural responses

Academic Editors: Motiki Meshack Mofokeng, Samson Tesfay and Salmina Mokgehle

Received: 11 February 2026
Revised: 23 March 2026
Accepted: 27 March 2026
Published: 30 March 2026

during subsequent extreme events [7,8]. While plasticity manages short-term volatility, the heritability of these plastic traits—often mediated via epigenetic mechanisms like DNA methylation—ensures that adaptive responses are transmitted to offspring, bypassing the slow pace of traditional genetic mutation [9,10].

Tomatoes (*Solanum lycopersicum* L.), a globally vital horticultural staple food, have already faced significant production disruptions due to these shifting climate patterns [11]. While phenotypic plasticity is a universal survival mechanism, the domestication of tomato has often traded this inherent adaptability for yield stability under high-input conditions, leaving modern varieties vulnerable to environmental volatility. Re-establishing this resilience through non-genetic interventions is therefore a critical priority for sustainable agriculture [12]. A pivotal factor in addressing these challenges is the nursery stage, where high-quality seedlings establish the foundation for improved root systems, nutrient uptake, and photosynthetic efficiency, ultimately driving higher crop yields [13]. Techniques such as seed ultrasonication serve as an effective pre-sowing treatment to improve germination and early-stage crop establishment. By physically modifying the seed coat to increase pore density, ultrasound enhances moisture uptake—a critical factor for uniform germination [14,15]. Beyond physical changes, it has been hypothesized that such mechanical stimuli could trigger internal regulatory shifts. For instance, observations in other species, such as winter wheat, suggest that priming events might be associated with temporary epigenetic modifications or altered gene expression, which could provide a biological advantage for accelerated growth [16]. While the specific heritability of these effects in tomato requires further investigation, these findings in related systems suggest a plausible mechanism for how early-stage priming might influence subsequent plant development or even intergenerational responses.

Modern seed priming is increasingly viewed as a high-precision component of integrated stress-management systems, moving beyond traditional 'wet-and-dry' methods toward targeted pre-conditioning [17]. Recent advancements highlight the importance of optimizing treatment intensity to trigger adaptive responses while avoiding metabolic fatigue [18]. Physical stimuli, such as ultrasound, offer a sustainable means of enhancing resource-use efficiency and stabilizing epigenetic responses [19]. By positioning priming within this framework, it is possible to transform erratic physiological responses into predictable gains in crop resilience [20]. In this study, we investigated the potential for cross-tolerance—a phenomenon in which exposure to one stimulus enhances a plant's defensive capacity against a distinct secondary stressor—by pairing mechanical stimulation (ultrasound) with osmotic stress (PEG 6000) [21].

By applying Euclidean distances and parameter variances in multidimensional space, the MVPi [4] integrates diverse phenotypic characteristics into one comprehensive marker. This approach streamlines genotype assessments by providing a systemic, rather than isolated, view of plant responses. Critically, investigations were conducted to determine whether these plastic responses can be transmitted to subsequent generations, thereby establishing a heritable "stress memory" to improve the resilience and productivity of offspring in increasingly arid environments [22].

The miniature cultivar 'Micro-Tom' tomato provides an ideal platform for exploring these intergenerational dynamics; its exceptionally short life cycle and compact architecture allow for the observation of multi-generational phenotypic stabilization within a significantly compressed timeframe compared to standard cultivars [23].

In this context, it is important to distinguish between the levels of phenotypic inheritance. Intragenerational plasticity refers to the somatic stress memory formed within the parental (F0) generation, while intergenerational plasticity describes the shifts observed in the immediate (F1) progeny. While some literature uses the term 'transgenerational' broadly, we define it strictly as effects persisting into the F2 generation and beyond, where

direct environmental exposure to the initial stressor can be ruled out. Given our focus on the F1 generation, this study primarily investigates intergenerational stress memory.

Building on these concepts, the objective of this research was to systematically evaluate the phenotypic plasticity and potential for intergenerational plasticity (IGP) in the tomato model system (*Solanum lycopersicum* L. cv. Micro-Tom). Operating within a dual-priming framework, this study employed PEG 6000 to simulate osmotic drought stimuli, alongside ultrasound as a physical seed-priming agent. The aim of this research included identifying how these divergent stressors induced immediate physiological and structural adaptations within a single generation.

2. Materials and Methods

2.1. Plant Material, Treatments, and Growing Conditions

Tomato (*Solanum lycopersicum* L. cv. Micro-Tom) plants, provided by the Hungarian University of Agriculture and Life Sciences (Institute of Genetics and Biotechnology), served as the experimental material. Since the initial quantity of seeds received was limited, the original seeds were grown out to produce and harvest an adequate quantity of seeds for the experiment.

For the ultrasound treatment, a total of 600 seeds were used, divided across three independent experimental runs with four 50-seed Petri dishes per run. The custom-built ultrasonicator [24] was operated at a resonant frequency of 30 kHz with a power output of 120 W for 5 min. To ensure treatment uniformity and reproducibility, seeds were positioned at a fixed vertical distance of 4.5 cm directly beneath the transducer. The treatment was conducted in a controlled air medium at a constant ambient temperature of 23 ± 2 °C to prevent thermal interference. For the baseline comparison, 200 seeds were used as controls (C). Following treatment, seeds were sown into individual pots (10 cm in diameter) containing forest soil (Mr. Garden, Agro CS Hungary Ltd., Salgótarján, Hungary) and cultivated under controlled conditions. Cultivation occurred in a growth room at 23 ± 2 °C under a 16 h light/8 h dark cycle. A 1:1 ratio of daylight and warm white fluorescent lamps provided a photosynthetic photon flux density (PPFD) of 130 µmol s^{-1} m^{-2}.

Three weeks post-sowing, both the control (C) and ultrasound-treated (US) groups were subdivided into two experimental subgroups. The first subgroup received standard irrigation (100 mL of tap water, twice weekly; C and USC), while the second subgroup was subjected to simulated drought stress (P and USP). Drought was induced by a single application of 100 mL of 20% *w/v* polyethylene glycol (PEG 6000 (Merck KGaA, Darmstadt, Germany), 200 g/L) solution. At this concentration, PEG-6000 provides an osmotic potential of approximately -0.5 MPa at 25 °C, which is a standard benchmark for simulating moderate to severe field drought in tomato studies. This was followed by a reduced irrigation regime of 50 mL of tap water, twice a week (Figure 1).

To assess intragenerational effects, seeds were harvested from physiologically mature parental berries, rinsed, and air-dried for 24 h before being stored at −20 °C for three months.

A total of 600 F1 seeds were then sown following the same, aforementioned protocol (without ultrasound treatment). Specifically, 100-100 seeds originating from the control (C) and PEG-treated (P) lineages were used, alongside 100-100 seeds harvested from both the ultrasound (USC) and the combined US-PEG-treated groups (USP). Three weeks post-sowing, seedlings derived from the control (C) and PEG-pretreated (P) lineages were subdivided into two experimental subgroups. The first subgroup was maintained under a standard irrigation regime (CC, PC), whereas the second was subjected to simulated drought stress (CP, PP), as previously detailed. Seedlings originating from the ultrasound (USC) and combined PEG-ultrasound (USP) groups were exclusively assigned to the drought stress treatment (USCP and USPP, respectively) (Figure 1).

https://doi.org/10.3390/horticulturae12040422

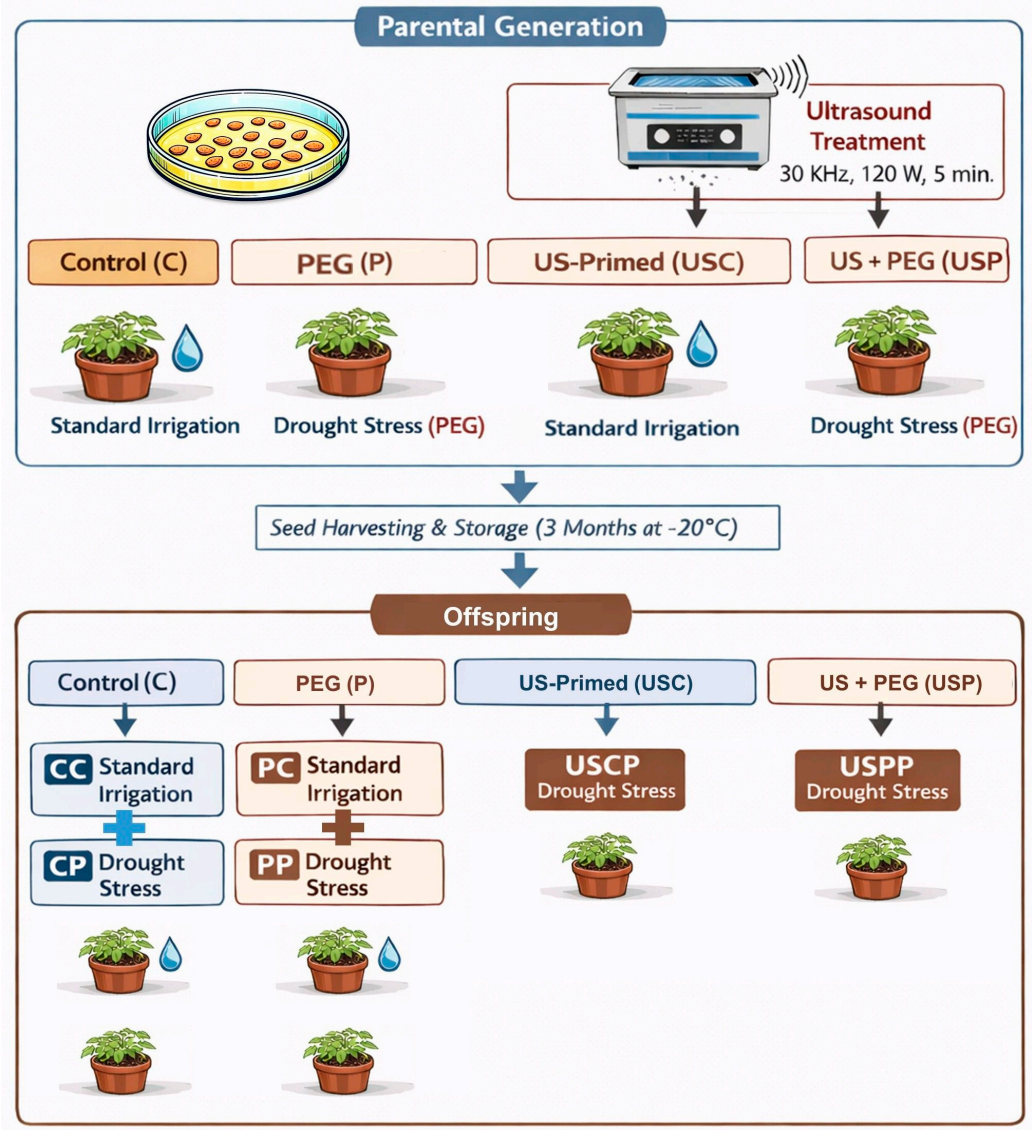

Figure 1. Visual overview of the two-generation experimental design used to study inherited phenotypic responses in Micro-Tom tomato plants. The methodology integrates a parental priming phase using ultrasound (US) and/or polyethylene glycol (PEG 6000), a simulated drought stress, with a progeny challenge using only PEG.

2.2. Data Collection and Statistical Analysis

Growth parameters (plant height and leaf number) were recorded weekly following drought induction in both generations. Phenological stages—from sprouting to fruit ripening—were documented for all plants. At maturity, yield metrics including berry count and seed production per fruit were documented. To ensure the robustness of the results, all plants (100 plants in each treatment) were included in the morphological and phenological analyses. No plants were excluded from the dataset, ensuring that the values reflect the full phenotypic variance of each treatment group. Each individual plant was grown in a separate pot, therefore serving as an independent biological replicate (experimental unit). All measurements (morphological and phenological) were recorded on a per-plant basis.

All individual trait data were analyzed using GraphPad Prism version 8.0 for Windows (GraphPad Software, Boston, MA, USA, www.graphpad.com). A One-way Analysis of Variance (ANOVA) was conducted to determine significant differences among the

treatment groups for each trait. Where a significant F-statistic was detected ($\alpha = 0.05$), post hoc analysis was performed using Tukey's Honestly Significant Difference (HSD) test.

A multivariate approach was employed to quantify overall phenotypic divergence using the Multivariate Plasticity Index (MVPi) as described by Pennachi et al. [4]. All raw trait data were normalized to account for different scales and units. The overall phenotypic dissimilarity between each pair of parental and offspring treatment groups was calculated using the Euclidean distance metric:

$$D_{ij} = \sqrt{\sum_{k=1}^{n} (X_{ik} - X_{jk})^2} \quad (1)$$

where D_{ij} is the Euclidean distance between parental group i and group j; X_{ik} is the normalized value of the k-th trait for group i; and n is the total number of traits measured [4].

To determine the relative importance of the different trait categories (morphological vs. temporal) in driving total divergence, the contribution weight of each category was calculated. This metric expresses the percentage that morphological or temporal traits contribute to the total MVPi value for each comparison (using the sum-of-squares approach; demonstrated through the computation of the morphological contribution weight):

$$\text{Contribution Weight}_{\text{Morphological}} = \frac{\text{MVPi}^2_{\text{Morphological}}}{\text{MVPi}^2_{\text{Morphological}} + \text{MVPi}^2_{\text{Temporal}}} \times 100 \quad (2)$$

This analysis identified whether physical structure or developmental timing was the primary factor in distinguishing the parental and offspring treatment groups. In the current literature, researchers typically use MVPi to compare different genotypes or species within the same environmental context or, on the contrary, generation of the same genotype or species across different environmental contexts [22,25–27].

Intergenerational Plasticity Ratio (IPR) is a logical extension of existing plasticity theory that represents a novel application for quantifying intergenerational plasticity (IGP).

$$\text{IPR} = \frac{\text{MVPi}_{\text{Offspring}}}{\text{MVPi}_{\text{Parental}}} \quad (3)$$

The IPR is intrinsically centered at 1.0, which represents the phenotypic identity point where offspring plasticity perfectly matches parental plasticity. Unlike empirical indices that rely on arbitrary thresholds, the IPR is a normalized ratio; therefore, any deviation from 1.0 represents a mathematical shift in the intergenerational strategy. An IPR > 1 indicates intragenerational priming or amplification, where the offspring generation has become more phenotypically divergent than its parents in response to the same stress. Meanwhile, an IPR < 1 suggests canalization or reduced plasticity, where the offspring generation is more "fixed" or less responsive than the parents. This new analytical framework for intergenerational experiments provides a more holistic approach to how the entire plant strategy has evolved or changed between generations, in contrast to comparing generations using simple mean trait values or individual trait plasticity indices (like RDPI) [28]. To assess the statistical significance and robustness of the Multivariate Plasticity Index (MVPi) and the newly proposed Intergenerational Plasticity Ratio (IPR), a bootstrapping procedure was performed. We employed the Bias-Corrected and Accelerated (BCa) bootstrap method with 1000 iterations in SPSS (IBM SPSS Statistics version 31, Armonk, NY, USA) to calculate 95% confidence intervals and *p*-values. This approach accounts for potential bias and skewness in the distribution of the multivariate indices. The significance of the IPR was determined by whether its 95% BCa confidence interval excluded 1.0 (the point of intergenerational identity). Any such exclusion was considered a statistically

significant shift ($p < 0.001$) in intergenerational plasticity, ensuring that observed amplification (IPR > 1) or canalization (IPR < 1) effects were not due to random sampling variation.

Although the experimental design included a combined treatment (ultrasound and drought), a one-way ANOVA was preferred over a factorial design to treat each stress scenario as a discrete experimental condition. This approach was chosen to facilitate the subsequent calculation of the MVPi and IPR indices, which specifically aim to integrate multivariate phenotypic variance into a single metric of intergenerational strategy, rather than isolating interaction effects between individual factors.

3. Results

3.1. Evaluation of the Parental Generation

Significant differences were observed across the four parental groups (C, P, USC, and USP) for all morphological traits measured, as indicated by the distinct significance grouping letters (a, b, c, d) within each row of Table 1.

Regarding vegetative growth, the USC group displayed the highest number of leaves (9.81 ± 1.31), followed by the control group (C, 8.5 ± 1.61), with P having the fewest (5.46 ± 1.14). In terms of height (mm), plants from the control group (C) were the tallest (129.77 ± 38.93), followed by USC (108.90 ± 27.55). P and USP treatments showed no significant difference from each other in height (55.18 ± 19.40 and 58.17 ± 19.12, respectively), but both were significantly shorter than C and USC.

Table 1. Means and standard deviations for morphological and temporal traits of four parental groups (C, P, USC, and USP). Values are presented as mean ± standard deviation. Different lowercase letters within the same row indicate significant differences between parental groups, as determined by Tukey's Honestly Significant Difference (HSD) post hoc test ($p < 0.05$).

	C	P	USC	USP
Morphological data				
Number of flowers/plant	5.86 ± 3.127 b	1.30 ± 0.48 d	8.71 ± 3.25 **a**	3.25 ± 1.86 c
Number of berries/plant	3.62 ± 1.99 **a**	1.00 ± 0.00 b	3.77 ± 1.75 **a**	1.18 ± 0.44 b
Number of seeds/berry	17.22 ± 3.98 b	0.23 ± 0.54 d	21.61 ± 4.56 **a**	0.97 ± 0.78 c
Number of leaves	8.50 ± 1.61 b	5.46 ± 1.14 d	9.81 ± 1.31 **a**	6.04 ± 0.07 c
Height (mm)	129.77 ± 38.93 **a**	55.18 ± 19.40 c	108.90 ± 27.55 b	58.17 ± 19.12 c
Temporal data (days)				
Sprouting	7.10 ± 0.12 **a**	6.89 ± 0.11 **a**	6.98 ± 0.09 **a**	7.09 ± 0.13 **a**
Beginning of flowering	79.59 ± 16.98 **a**	70.50 ± 22.32 b	55.31 ± 12.49 c	50.22 ± 9.87 d
Full blooming	89.21 ± 12.64 **a**	65.00 ± 20.75 c	64.14 ± 9.79 c	73.25 ± 21.88 b
Start of berry formation	92.29 ± 14.81 **a**	67.75 ± 29.02 b	64.47 ± 14.09 b	65.24 ± 17.24 b
Start of berry ripening	109.20 ± 5.19 **a**	91.33 ± 9.24 c	96.01 ± 9.32 b	89.52 ± 9.53 c
Full berry ripening	118.00 ± 0.70 **a**	118.00 ± 0.00 **a**	118.00 ± 0.00 **a**	118.01 ± 0.09 **a**

Regarding the number of flowers/plant, USC exhibited the highest number of flowers (8.71 ± 3.25), while P had the lowest (1.3 ± 0.48). A similar trend was observed regarding the average number of berries/plant and seeds/berry, where USC consistently produced the highest values (3.77 ± 1.75 and 21.61 ± 4.56, respectively), and P consistently produced the lowest (1.00 ± 0.00 and 0.23 ± 0.54, respectively). With regard to the temporal data, there was no significant difference among any of the four parental treatments for sprouting, all falling within the range of 6.89 ± 0.11 to 7.10 ± 0.12 days. However, a significant difference was found in flowering and ripening times. Significant variations were observed in the age (in days) at which plants reached various flowering and ripening stages across the parental treatment groups. The USP group began the flowering phase earliest

(50.22 ± 9.87 days); however, USC and P reached full bloom earlier than the other treatment groups (64.14 ± 9.79 and 65.00 ± 20.75 days). Conversely, the control group (C) consistently reached these developmental stages the latest. For berry development, the beginning of berry formation (days) and the beginning of berry ripening (days) both showed the C treatment initiating significantly later than all others (92.29 ± 14.81 and 109.20 ± 5.19, respectively). Interestingly, P, USC, and USP treatments did not differ significantly from each other at the beginning of berry formation. Finally, full ripening of berries (days) took place at the same time because there was no significant difference between the groups.

The Multivariate Plasticity Index (MVPi, Table 2) was calculated using the Euclidean distance formula to quantify overall phenotypic differences between four parental groups (C, P, USC, USP), integrating data from total, morphological, and temporal traits. The resulting distance matrix provides a measure of dissimilarity between each pair of groups; larger values indicate greater overall phenotypic divergence.

The calculated Euclidean distances varied between approximately 2.29 and 7.98, indicating a degree of plastic divergence among the treatment groups. All MVPi values are statistically significant ($p < 0.001$), as 95% BCa confidence intervals exclude the 0 baseline (total stability). The greatest overall phenotypic distance (Total MVPi) was observed between the C vs. P groups (7.98), indicating they are the most divergent pair across all measured traits. The C vs. USC comparison showed the lowest total distance (3.89), suggesting a higher degree of phenotypic similarity between these two parental treatment groups. This trend was largely driven by morphological traits, with C vs. P showing the largest distance (7.21), and C vs. USC showing the smallest (2.29). Temporal traits showed less variation in distance across comparisons, ranging narrowly from 3.15 to 3.42 (Table 2).

The contribution-weight analysis reveals which category of traits (morphological or temporal) drives the overall MVPi calculation for each parental comparison (Table 2). For the C vs. P and C vs. USP comparisons, the total phenotypic divergence was primarily driven by morphological traits, which accounted for the vast majority of the contribution (81.62% and 79.28%, respectively). Conversely, in the C vs. USC comparison, temporal traits were the dominant factor, contributing 65.54% of the total MVPi, while morphological traits contributed only 34.46%. This indicates that the primary difference between the C and USC groups lies in the timing of their development rather than in their physical structure.

Table 2. Multivariate Plasticity Index (MVPi) and relative contribution weights of morphological and temporal traits for the parental generation of *Solanum lycopersicum* (cv. Micro-Tom). Parental generation: C—Control group (standard irrigation, no stress/priming). P—PEG-treated group (osmotic/drought stress). USC—Ultrasound-primed group (no drought stress). USP—Ultrasound-primed group (osmotic/drought stress).

	C vs. P	C vs. USC	C vs. USP
MVPi			
Total	7.98	3.89	7.42
Morphological	7.21	2.29	6.61
Temporal	3.42	3.15	3.38
Contribution weight (%)			
Total	100.00	100.00	100.00
Morphological	81.62	34.46	79.28
Temporal	18.38	65.54	20.72

3.2. Evaluation of Progeny

In terms of physical development, the number of leaves varied significantly, with the USCP group producing the most leaves (7.02 ± 1.12) and CP the fewest (3.70 ± 1.81). For height (mm), the PC group was tallest (61.40 ± 10.86), while the CP group was shortest (35.40 ± 25.60) among all treatment groups.

Regarding the mean number of flowers/plant, the PP group exhibited the highest value (0.81 ± 0.1), while the USCP group had the lowest (0.12 ± 0.04), as seen in Table 3. A similar pattern was observed for the mean number of berries/plant, where the PC group produced significantly more berries (0.90 ± 0.14) compared to the lowest-yielding USCP group (0.08 ± 0.28).

Sprouting (days) was the only trait where all groups fell into the same significance group ('a'), indicating no significant difference in the time required for seeds to sprout across any of the six progeny treatment groups. However, significant variation was observed in flowering times. The PC group initiated flowering earliest (40.40 ± 15.4), while the CC group started latest (64.44 ± 25.86). For full blooming (days), the earliest group was USCP (53.50 ± 9.02), followed by groups with similar treatments, including PC (51.86 ± 6.12) and USPP (59.19 ± 13.93). The CC group reached full bloom the latest (70.78 ± 22.12).

All MVPi values are statistically significant ($p < 0.001$), as 95% BCa confidence intervals exclude the 0 baseline (total stability). The greatest overall phenotypic distance (Total MVPi, Table 4) was observed between the CC vs. USCP progeny groups (2.88), indicating they are the most divergent pair across all measured traits. The CC vs. USPP comparison showed the lowest total distance (1.85), suggesting the highest degree of phenotypic similarity among these five comparison groups. This pattern was largely driven by morphological traits, with the CC vs. USCP comparison yielding the largest distance (3.25) and the CC vs. USPP comparison yielding the smallest (0.77).

For most comparisons (CC vs. PC, CC vs. PP, CC vs. USCP), the total phenotypic divergence was predominantly driven by morphological traits, accounting for over 75% of the total contribution. A notable exception was the comparison between CC and USPP. In this case, temporal traits were the dominant factor, contributing 82.92% of the total MVPi, while morphological traits contributed only 17.08%. This indicates that the primary difference between the CC and USPP progeny types lies in their timing of development rather than their physical structure.

Table 3. Means and standard deviations for morphological and temporal traits of six progeny groups (CC, CP, PC, PP, USCP, and USPP). Values are presented as mean ± standard deviation. Different lowercase letters within the same row indicate significant differences between groups, as determined by Tukey's Honestly Significant Difference (HSD) post hoc test ($p < 0.05$). Traits sharing the same letter within a row are not statistically different from one another.

	CC	CP	PC	PP	USCP	USPP
Morphological data						
Number of flowers/plant	0.61 ± 0.12 c	0.32 ± 0.01 c	0.62 ± 0.11 c	0.81 ± 0.1 b	0.12 ± 0.04 **a**	0.45 ± 0.21 c
Number of berries/plant	0.41 ± 0.17 c	0.16 ± 0.23 d	0.90 ± 0.14 **a**	0.61 ± 0.26 c	0.08 ± 0.28 b	0.21 ± 0.43 c
Number of seeds/berry	1.48 ± 0.35 d	0.38 ± 0.12 b	4.20 ± 0.25 **a**	1.55 ± 0.17 d	2.20 ± 2.40 c	1.70 ± 2.32 d
Number of leaves	4.20 ± 2.17 b	3.70 ± 1.81 e	6.00 ± 1.19 **a**	5.10 ± 1.64 c	7.02 ± 1.12 f	6.51 ± 1.52 d
Height (mm)	43.5 ± 30.91 b	35.40 ± 25.60 d	61.40 ± 10.86 **a**	40.60 ± 12.45 c	42.23 ± 10.23 c	38.12 ± 12.10 c
Temporal data (days)						
Sprouting	7.23 ± 0.15 **a**	7.23 ± 0.57 **a**	7.01 ± 0.31 **a**	6.90 ± 0.46 **a**	7.29 ± 0.51 **a**	7.29 ± 0.48 **a**
Beginning of flowering	64.44 ± 25.86 a	59.70 ± 16.20 **a**	40.40 ± 15.4 b	46.50 ± 12.54 c	42.36 ± 13.25 b.c	49.57 ± 18.22 c
Full blooming	70.78 ± 22.12 c	61.51 ± 5.63 b	51.86 ± 6.12 **a**	69.52 ± 10.01 d	53.50 ± 9.02 **a**.b	59.19 ± 13.93 b
Start of berry formation	81.88 ± 23.82 **a**	62.70 ± 8.81 b	61.94 ± 7.72 b	56.81 ± 7.31 c	60.33 ± 7.31 b	68.36 ± 13.82 d
Start of berry ripening	95.28 ± 14.51 **a**	87.90 ± 8.41 b	87.69 ± 9.83 b	83.89 ± 8.94 b	88.33 ± 4.87 b	94.18 ± 12.758 c
Full berry ripening	107.89 ± 21.36 **a**	121.5 ± 18.13 b	100.40 ± 15.14 **a**	121.70 ± 12.81 b	105.00 ± 13.01 **a**	108.00 ± 14.10 c

https://doi.org/10.3390/horticulturae12040422

Table 4. Multivariate Plasticity Index (MVPi) and Relative Contribution Weights of Morphological and Temporal Traits for the Offspring Generation of *Solanum lycopersicum* (cv. Micro-Tom). Offspring generation comparisons: where the first letters denote the parental treatment lineage (C, P, USC, or USP), and the second denotes the offspring treatment (C or P).

	CC vs. PC	CC vs. PP	CC vs. USCP	CC vs. USPP
MVPi				
Total	2.09	2.32	2.88	1.85
Morphological	2.47	2.57	3.25	0.77
Temporal	1.32	1.09	1.51	1.69
Contribution weight (%)				
Total	100.00	100.00	100.00	100.00
Morphological	77.86	84.72	82.26	17.08
Temporal	22.14	15.28	17.74	82.92

3.3. Evaluation of Intergenerational Plasticity Ratio (IPR)

All IPR values were statistically significant ($p < 0.001$), as 95% BCa confidence intervals excluded the 1.0 baseline (intergenerational identity). The IPR values revealed a predominant trend of intergenerational canalization across most offspring comparisons (Table 5). For the PC vs. P, PP vs. P, and USPP vs. USP lineages, all IPR values were consistently <1.0, indicating that offspring phenotypic divergence was significantly reduced relative to the parental baseline. This reduction was most pronounced in the USPP vs. USP lineage (Total IPR = 0.25), where a sharp contraction in morphological plasticity (IPR = 0.12) suggests a move toward a more "fixed" or robust phenotype in the offspring.

A notable exception to this trend was observed in the USCP vs. USC comparison. While the total and temporal strategies remained canalized (IPR < 1.0), the morphological IPR reached 1.42. This indicates a localized intergenerational amplification, where morphological traits became more phenotypically divergent in the offspring generation than in the parents, suggesting a specific priming effect or increased sensitivity in structural development despite a more stable developmental timing.

Table 5. The Intergenerational Plasticity Ratio (IPR), comparing the magnitude of offspring plasticity (F1) relative to parental plasticity (P0) across various treatment lineages. The comparisons highlight how the magnitude of phenotypic changes (measured by MVPi) is inherited or modified across generations following different parental stress and priming conditions.

	PC vs. P	PP vs. P	USCP vs. USC	USPP vs. USP
Total	0.26	0.29	0.74	0.25
Morphological	0.34	0.36	1.42	0.12
Temporal	0.39	0.32	0.48	0.50

4. Discussion

The comprehensive evaluation of the parental and offspring generations utilized both univariate (Tukey's HSD test) and multivariate (Multivariate Plasticity Index, MVPi) approaches to quantify phenotypic diversity. The integration of these methods provides a robust understanding of divergence, which is essential for guiding future priming strategies. Our results indicate significant phenotypic changes within a single growing season and across generations, demonstrating both intragenerational and intergenerational plasticity and a complex interaction between them in response to environmental stressors.

In the parental generation, the high degree of divergence observed between the Control (C) and PEG-treated (P) groups (Total MVPi: 7.98) underscores a robust intragenerational response. The P group exhibited a significant reduction in vegetative and reproductive outputs (lowest leaf count, flower number, and berry yield). This phenomenon occurs because plants do not merely suffer a passive loss of growth due to a lack of water; instead, they execute an active genetic program to intentionally repress growth as a proactive survival adaptation. This shift is governed by a sophisticated "growth-survival" trade-off mechanism that reallocates energy from biomass production to protective metabolic pathways [29]. This conservative strategy is an evolved response to unpredictable environments. By limiting their size and reproductive effort, plants minimize their transpirational water loss and energy demands, thereby increasing the probability of surviving long enough to reproduce once conditions improve [30,31].

Interestingly, the USC group displayed a unique strategy: while morphologically similar to the control, its primary divergence was temporal. This suggests an adaptive mechanism in which the plant maintains its physical structure while shifting its phenological clock to ensure reproductive success before conditions deteriorate [32–34]. By reallocating resources to accelerate flowering, the plant effectively optimizes its reproductive potential [35–37].

The evaluation of the progeny is consistent with the potential transmission of environmental experiences to the next generation, a characteristic pattern of intergenerational plasticity. However, the magnitude of this divergence was generally lower than that was seen in the parents. Recent findings on stress memory supported the theory of a "buffering" effect, in which epigenetic marks are largely erased after fertilization. This reset is an evolutionary safeguard against the metabolic costs of inheriting "memories" of stresses the next generation may never encounter [32,38,39].

The primary advantage of the IPR over conventional univariate trait analysis is its ability to quantify the systemic shift in adaptive strategy across generations. While traditional methods compare individual means (e.g., height or yield) in isolation, the IPR integrates these into a single value that identifies whether an entire generation has become more plastic (amplification) or more stable (canalization). Biologically, this allows us to distinguish between a 'reactive' parental generation and a 'pre-conditioned' offspring generation, providing a more comprehensive view of how stress memory reconfigures the plant's total life-history strategy rather than just its individual parts. The consistently low Intergenerational Plasticity Ratios (IPRs, below 1.0) for both PC and PP offspring relative to the parental generation (P) suggested an intergenerational reduction in systemic plasticity. This indicated that parental environmental experience may act as a canalizing force, narrowing the phenotypic plasticity in subsequent generations and potentially favoring a more stable, pre-conditioned developmental strategy over the high environmental responsiveness observed in the parents. The consistent reduction in IPRs below 1.0 across both morphological and temporal traits aligns with the theory of intragenerational canalization, in which parental environmental cues lead to a more constrained but potentially optimized phenotype in the offspring [40–42].

A notable finding was the USCP group, which showed a morphological IPR of 1.42 relative to its parent. This indicates that the offspring exhibited greater morphological divergence than the parental generation itself. This "intergenerational amplification" is potentially associated with epigenetic priming, where the parental stress (USC) may have pre-conditioned the progeny (USCP) to respond more drastically to their own environment. These results suggest that ultrasound treatment could act as a non-specific priming stimulus, potentially preparing plants' internal signaling pathways for heightened readiness to subsequent abiotic challenges [43]. Ultrasound is a mechanical stressor that has been shown to trigger a general 'alert' state in plants. Recent research highlights that such

priming can induce stress-responsive proteins and antioxidants that are not stress-specific but provide a broad protective buffer against various future threats, including osmotic stress [44]. The transition from mechanical priming (ultrasound) to drought tolerance (PEG) is likely facilitated by shared signaling molecules. For example, ultrasound is known to stimulate calcium signaling and antioxidant pathways, mitigating reactive oxygen species (ROS) in the parental generation, which are the same pathways required for drought response in the offspring. This 'shared language' of stress may allow for cross-tolerance [45,46].

Furthermore, by potentially fine-tuning gene expression—such as upregulating stress-responsive pathways—non-genetic regulatory shifts could contribute to yield stability in volatile climates. Such mechanisms may serve to reduce the 'yield gap' caused by environmental fluctuations [47]. These theoretical frameworks provide a plausible context for the phenotypic changes observed in our progeny groups, suggesting that early-stage priming might influence a plant's ability to navigate environmental stressors over time.

The contribution weight analysis revealed a significant distinction between what changed and when it changed. In the parental generation, stress primarily drove morphological changes (over 79% for P and USP). However, in the CC vs. USPP progeny comparison, the divergence was almost entirely temporal (82.92%). This indicates that intergenerational plasticity favored 'stress avoidance'—a sophisticated phenological adaptation where plants use inherited memory to 'escape' terminal stressors through optimized timing [35,48]. While effective for maintaining yield stability, this accelerated life cycle often necessitates a trade-off, where vegetative biomass is sacrificed to ensure survival and successful seed production under volatile climatic conditions [49]. Consequently, further research is required to optimize these phenological advances so that they do not compromise fruit quality or total commercial yield. In our study, the observed phenological shift in the USCP group was consistent with a classic 'escape' or 'disaster-avoidance' strategy. By prioritizing rapid development and maintaining a relatively robust leaf count (7.02), these plants ensure survival and the potential for at least minimal seed set under severe stress. However, this survival mechanism clearly comes at a significant cost to horticultural value, as fruit yield was nearly eliminated (flowers: 0.12, fruits: 0.08). While this strategy is evolutionarily successful for species persistence, it highlights a critical challenge for 'epibreeding' in agriculture: The need to balance stress-induced phenological plasticity with the preservation of harvestable yield. Future research should focus on optimizing priming intensities to trigger resilience without crossing the threshold into total reproductive sacrifice. While the contribution weight analysis provides a clear mathematical distinction between morphological and temporal shifts, we acknowledge that these categories are physiologically interdependent. Phenological timing often dictates the window available for morphological development, and conversely, biomass accumulation can influence the transition to reproductive stages. Therefore, our interpretation of 'dominance' refers to the primary axis of phenotypic divergence captured by the MVPi, rather than suggesting these traits operate as entirely independent biological modules.

While the use of the 'Micro-Tom' tomato cultivar as a model system provided a robust framework for assessing both vegetative and reproductive plasticity across generations, several limitations should be noted. A primary strength of this study includes the application of the MVPi to capture the non-linear relationship between morphology and phenology; however, the diminutive size and rapid life cycle of 'Micro-Tom' may not fully reflect the resource allocation strategies of full-sized indeterminate tomato cultivars used in commercial agriculture. Furthermore, this study focused on the first offspring generation (F1); while we observed significant intergenerational cross-tolerance, it remains to be seen if these ultrasound-induced "epigenetic legacies" persist into the F2 generation or if the observed "buffering" effect results in a complete reset of the stress memory [32,39].

Additionally, while the phenotypic divergence in berry yield suggests a strategic resource reallocation, the underlying molecular mechanisms, specifically the extent of DNA methylation or histone modifications following mechanical priming, were not directly quantified. Future research utilizing large-scale field trials and methylome profiling is required to determine the scalability of ultrasound-based "epibreeding" for enhancing long-term yield stability across diverse horticultural environments [43,47,50].

The non-symmetrical F1 design employed here was prioritized to investigate the persistence of ultrasound-induced priming specifically under drought conditions. However, this structure poses a challenge to unravel parental inheritance from immediate environmental influences in certain groups. While the IPR index effectively captures the magnitude of the phenotypic shift, the response observed in the USCP and USPP groups may reflect a cumulative effect of both parental 'memory' and direct environmental stress. Consequently, these intergenerational trends should be interpreted as an integrated response, with future studies requiring a full factorial design to more precisely isolate the individual contributions of parental versus environmental drivers.

While the IPR framework and phenotypic results provide strong evidence for intergenerational adaptation, certain limitations warrant further investigation. First, the proposed mechanisms for ultrasound-induced 'epibreeding' and signaling readiness are based on phenotypic outcomes and established literature; direct molecular validation, such as gene expression (RT-qPCR) or DNA methylation analysis, would be necessary to confirm the specific epigenetic pathways involved. Second, our findings are based on a single cultivar (*Solanum lycopersicum* L. cv. Micro-Tom). Additionally, while the IPR findings suggest intergenerational amplification or canalization, these results should be interpreted cautiously until confirmed across multiple independent priming events to ensure broader reproducibility. As phenotypic plasticity can vary significantly between genotypes, future studies involving diverse tomato cultivars or wild relatives are needed to determine the broader applicability and genetic conservation of these intergenerational strategies. Addressing these gaps will further refine the use of ultrasound as a scalable tool for crop resilience.

Beyond the theoretical implications for plant memory, these findings provide a preliminary framework for exploring sustainable, climate-resilient horticulture. The evidence that ultrasound priming in 'Micro-Tom' can trigger intergenerational responses to osmotic stress (PEG) suggests a potential non-chemical, low-cost approach for enhancing crop robustness. This phenotypic priming utilizes the plant's innate plasticity, offering an alternative to traditional breeding for improving stability in volatile environments. Specifically, the observed temporal divergence—where plants accelerated their life cycle—illustrates a potential mechanism for stress avoidance. While the scalability of mechanical priming requires further testing across diverse genotypes and field conditions, these results highlight the possibility of integrating pre-sowing treatments into seed-conditioning protocols. Such strategies could eventually contribute to reducing the 'yield gap' by optimizing phenological timing without the metabolic burden of permanent structural changes [33,35,47].

5. Conclusions

The integration of univariate and multivariate approaches provides a comprehensive perspective on the complexities of plant responses, as highlighted in this work. While individual trait analyses provided specific phenotypic benchmarks, the Multivariate Plasticity Index (MVPi) offered a robust framework for quantifying overall phenotypic divergence and characterizing variance in future generations. Our results suggest a potential

'intergenerational trade-off': whereas parental generations exhibited significant morphological reductions under immediate stress (intragenerational plasticity), this was followed by more efficient temporal adjustments in the offspring (intergenerational plasticity).

The comparison of PC and PP offspring groups with their respective parental generation (P) reinforced this pattern, demonstrating an intergenerational canalization of the systemic plastic response. The consistently low Intergenerational Plasticity Ratios (well below 1.0) indicated that the offspring's overall divergence is significantly lower than the observed stress-induced divergence found within the parental generation. This suggests that the offspring were buffered against wide-ranging phenotypic shifts, effectively "locking in" an optimized, stable strategy rather than maintaining high, potentially costly, systemic plasticity [40–42].

Crucially, the observed intergenerational amplification in the USCP progeny suggests that parental environmental experiences could influence the phenotypic range of offspring, offering a potential mechanism for rapid response in volatile climates. These findings highlight ultrasound-based mechanical priming as a plausible "epibreeding" tool, enabling fruit-bearing crops like 'Micro-Tom' tomato to "escape" abiotic stressors through optimized phenology. Mechanical priming via ultrasound may have triggered an intergenerational strategic shift, in which plants switch from resource-intensive morphological defense in the parental generation to cost-effective phenological "escape" in the progeny. Ultimately, this research offers a preliminary framework for exploring how crop development might be synchronized with increasingly unpredictable seasonal patterns, suggesting a pathway toward yield stability that minimizes the metabolic costs of permanent structural change.

Author Contributions: Conceptualization, J.D.; methodology, J.D. and D.F.; formal analysis, J.D. and D.F.; investigation, J.D. and D.F.; data curation, J.D. and D.F.; writing—original draft preparation, D.F.; writing—review and editing, J.D.; visualization, D.F.; supervision, J.D.; funding acquisition, J.D. All authors have read and agreed to the published version of the manuscript.

Funding: Project no. TKP2021-EGA-20 (Biotechnology) has been implemented with support provided by the National Research, Development and Innovation Fund of Hungary, financed under the TKP2021-EGA funding scheme. Supported by the University of Debrecen Program for Scientific Publication.

Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

MVPi	Multivariate Plasticity Index
IPR	Intergenerational Plasticity Ratio
PEG	Polyethylene glycol 6000
US	Ultrasound
C	Control group (parental generation, normal watering)
USC	Ultrasound-treated group (parental generation, normal watering)
P	PEG-treated group (parental generation, reduced watering)
USP	Ultrasound and PEG-treated group (parental generation, reduced watering)
CC	Offspring generation of C, normal watering
CP	Offspring generation of C, PEG-treatment, reduced watering
PC	Offspring generation of P, normal watering
PP	Offspring generation of P, PEG-treatment, reduced watering
USCP	Offspring generation of USC, PEG-treatment, reduced watering

USPP Offspring generation of USP, PEG-treatment, reduced watering

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