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Parental effects on progeny: intergenerational phenotypic plasticity in potato plants

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Abstract
Previous studies have already supported the ability of plants to pass on newly acquired traits to their offspring, thereby increasing their resilience and fitness. However, these basic researches mostly focused on environmental impacts on plants and the heritability of the induced effects. Therefore, we tried to develop a method, using ultrasound - that could stimulate plant growth and development- in combination with an abiotic stress that occurs due to climate change. In this experimental study, one of the most significant stresses resulting from climate change, the drought stress, was selected, which we triggered by applying polyethylene glycol. Ultrasound as a stimulant on potato plants was applied under controlled conditions. The possible heritability of increased drought tolerance and the associated morphological and temporal changes were investigated. Based on the results, drought treatment had a positive after-effect on the second generation (progeny) under stress conditions. This positive after-effect was significantly amplified by the use of ultrasound in the parental generation. Furthermore, ultrasound itself had a preparatory effect on clonally propagated plants. Therefore, implementation of ultrasound treatment of the parental generation may offer a cost-effective alternative technology for modern agriculture to address the adverse effects of climate change in the progeny.

Keywords: climate change, drought, polyethylene glycol, *Solanum tuberosum* L., ultrasound, yield

Introduction

Due to their sessile nature, plants need the inherent ability to change their physical traits or phenotype in order to ensure their fitness in an ever-changing world. This phenomenon is called plasticity in the classic sense (sometimes called 'phenotypic flexibility'), that involves responding in a consistent way to various environmental factors during a lifetime. Plasticity can occur through multiple pathways including cellular, physiological and behavioral mechanisms, in which epigenetic processes such as modifications in DNA methylation patterns or changes in chromatin structure play an important role. These epigenetic factors may be transmitted from parent to subsequent generations that may cause changes in offspring phenotype induced via a consequent cascade of developmental effects [1-2]. Furthermore, over several generations, the magnitude of transgenerational plasticity effect may increase or be modulated by different environmental factors. Since this field of science is still relatively young and has only recently become a focus of research, there may be misunderstandings in the jargon as terminology related to this phenomenon is still evolving. 'Intergenerational' plasticity refers to the effects of parents on the immediate offspring, while 'transgenerational" plasticity is the concept of these effects spanning over multiple generations [3]. Clear evidence of transgenerational inheritance of epigenetic changes that may cause phenotypic plasticity in the absence of stress stimuli to the progeny remains limited, however, intergenerational epigenetic inheritance has been demonstrated in research [4-6]. The ideology of the transmittance of environmental effects (either from biotic or abiotic stresses) to the progeny is of interest due to the possibility of providing heritable variation on which natural selection can act [7]. Even if these effects may fade out over a single or multiple generations, it could still be interesting from an evolutionary perspective as these effects may play an important role in ensuring the populations' fitness in fluctuating environments.

In recent years, drought periods are becoming more frequent and longer as a result of climate change causing a major challenge to potato production worldwide as their shallow root system makes them one of the most drought sensitive species [8]. Furthermore, key biochemical and physiological processes are inhibited via drought leading to poor performance and tuber yield loss. It is also worth noting that the severity of this effect largely depends not only on the drought episode but on the plant also, i.e. the growth stage and cultivar

[9]. Under non-stressed conditions, drought pre-treatment reduced yield loss in the first tuber progeny according to Macko-Podgórni et al. [10].

Various physical factors or abiotic stresses are employed to enhance yield and improve the overall fitness of plans in modern agriculture, including electromagnetic fields, different kinds of radiation, laser light and ultrasound [11-12]. Although these factors do not cause chemical composition alterations of reproductive materials but may have an impact on physiological and chronological processes. Compared to chemical responses, the usage of physical signals including acoustic waves that propagate through a medium transmitting energy promote a swift and efficient adaptation to environmental changes [13]. Ultrasound can stimulate *in vitro* growth and development of potato plants and influence various physiological and biochemical processes including seed germination, shoot development, root growth, tuber propagation, signal transduction pathways, enzyme and hormone activity [14-15]. However, studies on the ultrasonication of plants have the biggest limitation of knowledge as the information available of the experiments are often incomplete (e.g. missing data including volume, power, frequency etc. on the properties of the ultrasound used) [16].

Material and Method

Plant material and treatment of in vitro plantlets

Pre-established *in vitro* cultures of *Solanum tuberosum* L. cv. Desirée were used as a source of explants for the experiment. The *in vitro* growing conditions and media composition for the plantlets were described earlier by Teixeira da Silva et al. [14].

Single-node explants were excised, then transferred into 50 ml glass-beakers containing 40 ml of liquid plant-growth regulator-free (PGR-free) Murashige and Skoog (MS) [17] medium under sterile conditions (100 explants per beaker). A total of eight beakers were then transferred simultaneously into an ultrasonicator (Elmasonic X-tra 30 H; Elma Schmidbauer GmbH, Singen, Germany) and immersed into distilled water. The temperature of the water was kept constant at 25°C. The frequency of the piezoelectric ultrasonicator was set to 35 kHz (70 W). The treatments lasted for 20 minutes, after which the ultrasonicated explants were placed into 400 ml glass jars containing 50 ml of solid, PGR-free MS media supplemented with 5% polyethylene-glycol (PEG6000, 8 mM/L). The explants for the control group were also placed into liquid MS media for 20 minutes, then transferred onto solid MS media (PGR and PEG-free), but were not exposed to ultrasound treatment. The jar type, explant quantity/vessel (20 explants per vessel) and medium quantity/vessel were always the same throughout the *in vitro* phases. The pH of the media was set to 5.8 before autoclaving at 121°C and 1.2 bar for 15 minutes. The cultures were maintained inside a culture room under controlled conditions with a 16/8 h photoperiod at a light intensity of 80–106 µmol s^{-1} m^{-2}, provided by a 1:1 ratio of warm white and daylight fluorescent lamps at a temperature of 23 ± 2°C. After 4 weeks of cultivation, the potato plantlets were transferred onto fresh media (PGR and PEG-free MS media for the control group, and PGR-free MS media supplemented with 5% PEG for the treated group) once again (for 4 weeks).

Ex vitro acclimatization and growing of potatoes

8 weeks after the start of the experiment the plantlets were transferred onto commercial garden soil (Mr. Garden, Agro CS Hungary Ltd.; pH 5.5, 0.1 m/m% N, 0.01 m/m% P_2O_5, 0.03 m/m% K_2O, 75.0 m/m% dry organic matter) in 4 L pots after carefully washing off the remaining media from the roots with normal tap water. The acclimatization process lasted for 3 weeks of which the pots were covered in plastic wraps to ensure adequate humidity levels. On the 12th week, the two groups (control and US-treated) were split into two sub-groups. The first group was irrigated with normal tap water throughout the experiment (300 ml, 2 times per week). However, the second sub-group was irrigated with a 20% PEG solution (300 ml, 32 mOsm/L, 32 mM/L) for the first watering, then received half as much water as the control group (150 ml tap water) all throughout the experiment (Figure 1.). The climate room was set to a constant 23 ± 2°C, with a 16/8 h photoperiod. The light intensity was 130 µmol s^{-1} m^{-2} provided by a 1:1:1 ratio of daylight, flora and warm white, fluorescent lamps.

After 28 weeks, tubers were collected and stored in paper bags inside a climate chamber at 4 ± 1°C for four months. Tubers were then planted in pots with commercial garden soil and grown in a climate room with identical conditions as the previous generation. The second generation was treated with 300 ml of 20% PEG solution on the 4th week after sprouting, except for the absolute control group (C-C-C), as it only received 300 ml tap water. The treatment groups that received PEG solution were then watered with 150 ml tap water twice per week, whereas the control group (C-C-C) received 300 ml water at the same time intervals.

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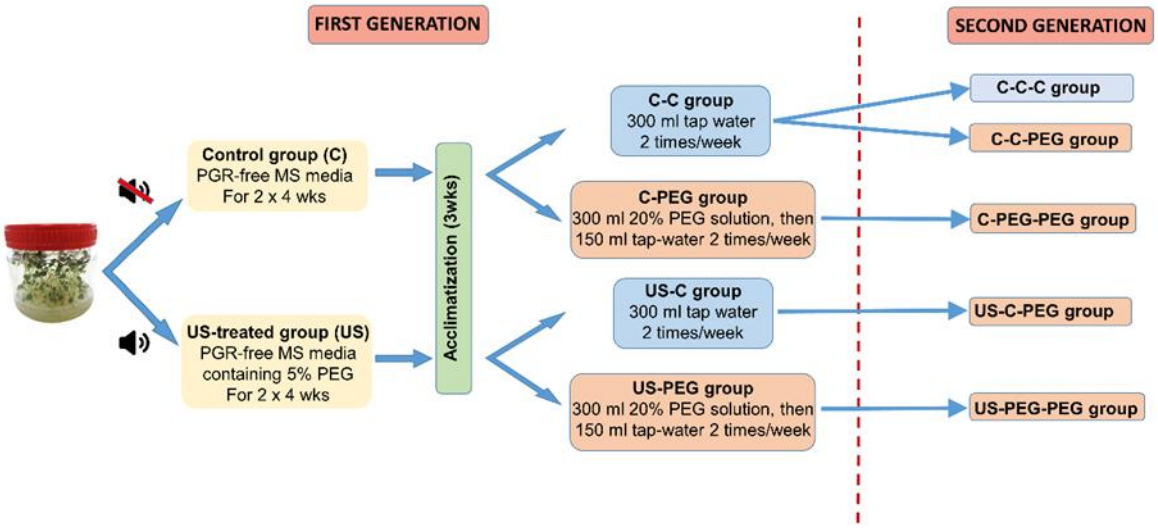

Figure 1. Schematic illustration of treatment regimen. Abbreviations: PGR – Plant growth regulator; MS - Murashige and Skoog medium; PEG- polyethylene-glycol 6000; C-C and C-C-C groups – absolute control groups in the first and second generations, respectively; C-PEG group – only received PEG treatment after acclimatization; US-C group – only received US treatment in the *in vitro* phase; US-PEG group – received US and PEG treatment in the *in vitro* phase and another PEG treatment after acclimatization; C-C-PEG group – only received PEG treatment in the second generation; C-PEG-PEG – received PEG treatment after acclimatization and during the second generation; US-C-PEG – only received US treatment in the *in vitro* phase and PEG treatment during the second generation; US-PEG-PEG – received US and PEG treatment in the *in vitro* phase and PEG treatment after acclimatization and during the second generation.

Data collection and statistical analysis

After acclimatization, the following data were collected from the first/parental and second generation: number of tubers produced, tubers total weight (g), plant height (mm) number of leaves were measured 28 weeks after the start of the experiment (100 plants/treatment group). For the second generation the timing of tuber sprouting and the onset of stolon formation were also recorded (in days). The obtained morphological data were subjected to statistical analysis via one-way ANOVA and Tukey's B test ($p < 0.05$) using SPSS for Windows software (SPSS®, version 25.0) and the results were presented using LabPlot software (Version 2.11.1) [18].

Results and Discussion

Morphological results of the parental generation

28 weeks after the start of the experiment, the C-C group included significantly the highest plants with an average height of 251.7 ± 7.5 mm, followed by the US-C treatment group with 196.4 ± 3.6 mm. The highest number of leaves was recorded for the C-C and US-C groups, which did not differ significantly from each other (29.1 ± 1.6 and 30.7 ± 1.6 respectively), and the lowest was counted for the C-PEG and US-PEG groups (17.0 ± 0.8 and 19.5 ± 0.4 respectively) (Figure 2.).

US-C treatment resulted in significantly ($p < 0.05$) the highest mean number of tubers with a value of 7.1 ± 0.4 tubers. The lowest mean number of tubers were recorded in two treatment groups with no significant difference between them: 4.3 ± 0.2 tubers for C-PEG and 3.9 ± 0.1 tubers for US-PEG treatment groups were counted, respectively (Figure 2.).

The mean total weight of tubers ranged from 10.6 ± 0.6 g to 3.4 ± 0.1 g per pot, where US-C resulted in the highest tuber weight, and the least tuber weight was achieved in the US-PEG group (that did not differ significantly from the C-PEG group).

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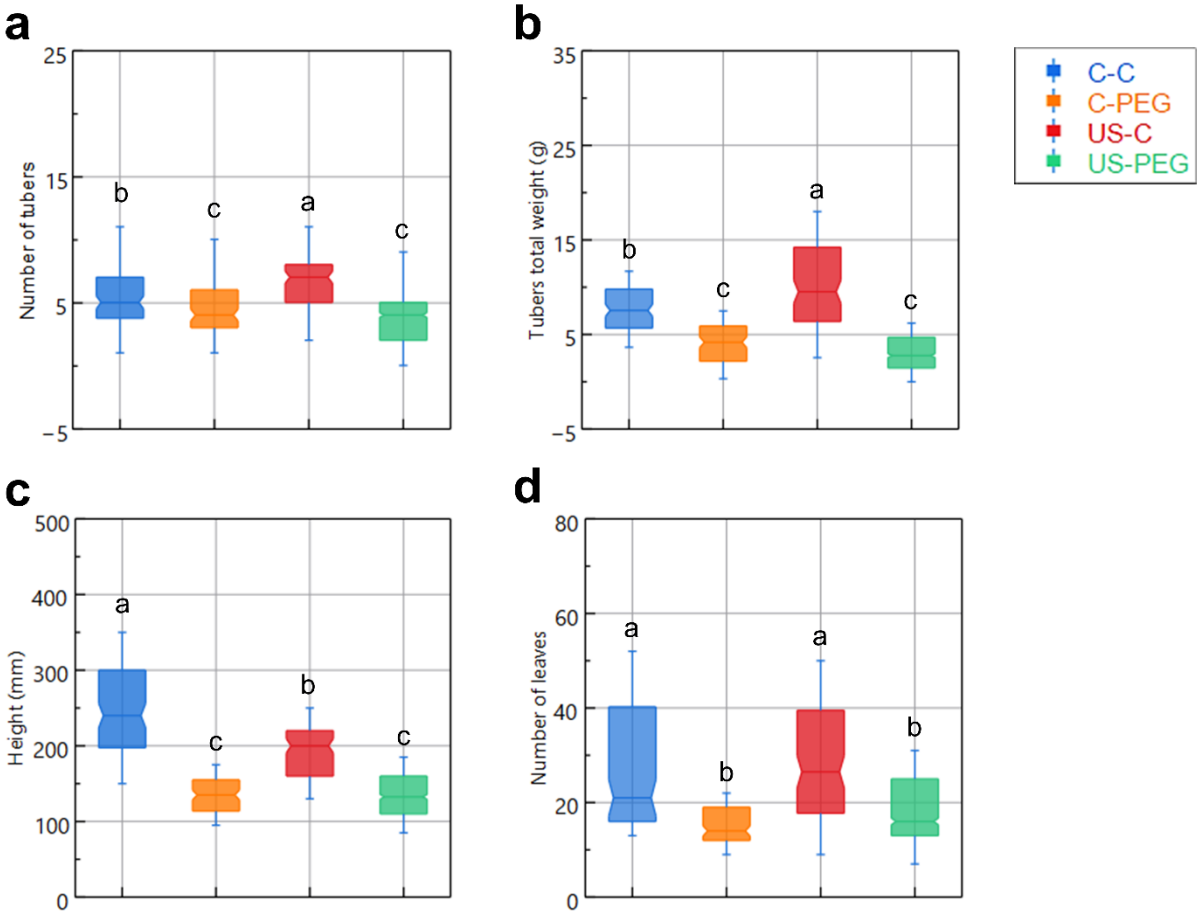

Figure 2. Mean values of measured parameters of the first/parental generation (a: number of tubers per plant, b: tubers total weight per plant (g), c: plant height in mm, d: number of leaves per plant). Different lower-case letters above the error bars indicate significant differences at the 0.05 level (one-way ANOVA and post hoc Tukey's B test results).

Morphological results of the second generation

The effects of different abiotic stresses for the second generation were evaluated at the end of the experiment (28 weeks). In terms of plant height, the highest potato shoots were recorded for the absolute control group (C-C-C) with an average 145.7 ± 21.9 mm, and the lowest shoots were observed for the treatment group that only received PEG treatment in the second generation (C-C-PEG; 77.9 ± 25.7 mm). US-PEG-PEG performed the best in terms of number of leaves per plant with a value of 12.9 ± 1.2, but this outcome was not significantly different from those of C-C-C and C-PEG-PEG (Figure 3.).

The highest mean number of tubers and total weight of tubers were achieved in the US-PEG-PEG treatment group with values of 2.9 ± 0.3 and 7.7 ± 1.9 g respectively (Figure 3.).

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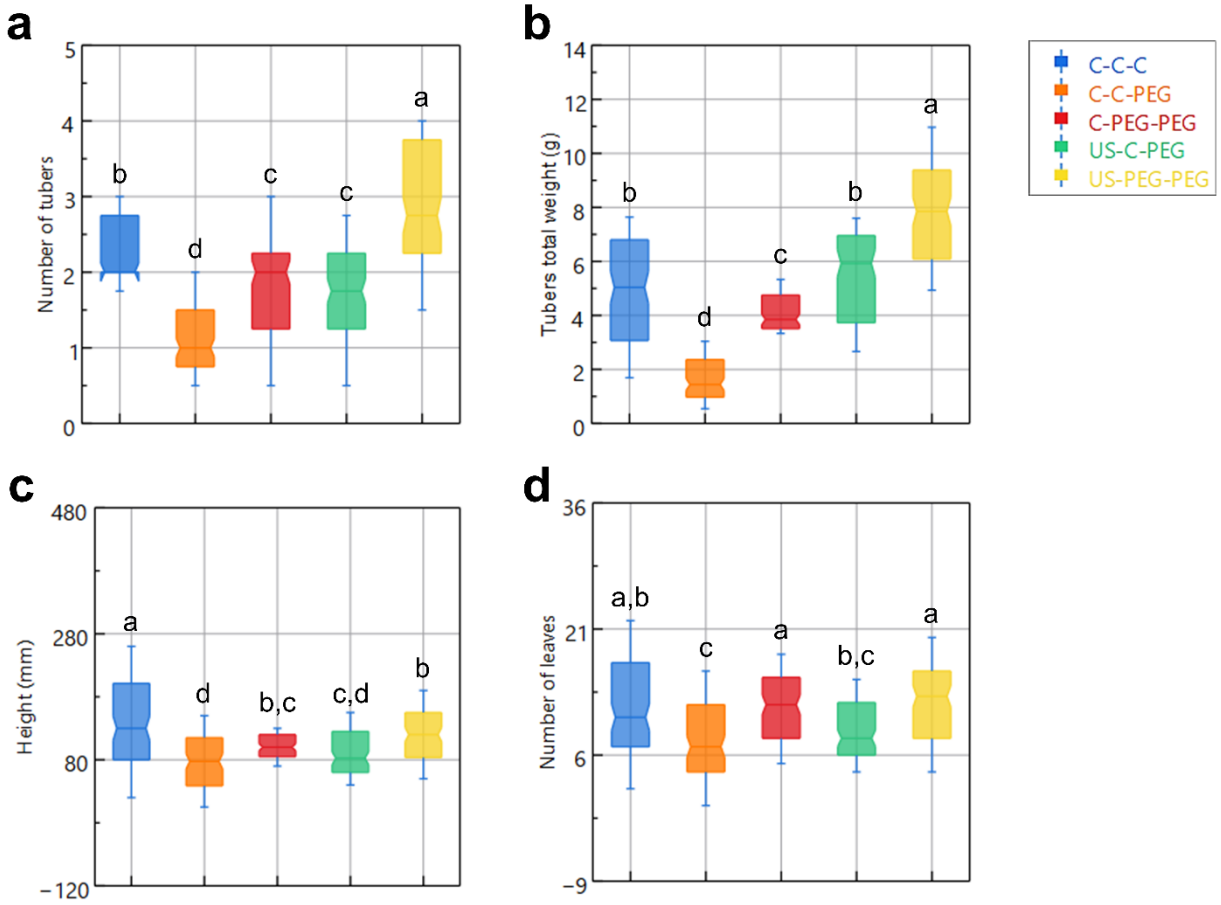

Figure 3. Mean values of measured parameters of the second generation (a: number of tubers per plant, b: tubers total weight per plant (g), c: plant height in mm, d: number of leaves per plant). Different lower-case letters above the error bars indicate significant differences at the 0.05 level (one-way ANOVA and post hoc Tukey's B test results).

Regarding the temporal aspects of the effect of previous treatment in the parental/first generation on tuber sprouting, C-PEG-PEG and US-PEG-PEG treatment groups sprouted significantly the earliest compared to the other treatment groups (Table 1.). With regards to stolons, US-PEG-PEG developed stolons the earliest (38.1 ± 1.0 days) among all treatments with a significant difference compared to the absolute control group (C-C-C, 45.0 ± 2.3 days) (Table 1.).

Table 1. Mean values of measured temporal data of the second generation at the 0.05 level (one-way ANOVA and post hoc Tukey's B test results).

Treatment	Tuber sprouting (days)	Stolon formation (days)
C-C-C	13.5 ± 0.9 a	45.0 ± 2.3 a
C-C-PEG	13.3 ± 1.0 a	39.5 ± 1.8 ab
C-PEG-PEG	7.3 ± 0.5 c	41.1 ± 2.0 ab
US-C-PEG	11.4 ± 0.6 b	41.0 ± 1.6 ab
US-PEG-PEG	6.7 ± 0.4 c	38.4 ± 1.0 b

Discussion

Epigenetic variations that can cause phenotypic plasticity may occur stochastically or can be induced via environmental stresses, for example, drought periods associated with climate change. Numerous studies investigated the transmittance of epigenetic markers through multiple generations by both sexual and asexual

reproduction [19]. It is recently increasingly researched whether if this form of heritable variability provides an opportunity on which natural selection can act on. However, the question of whether we can observe any inherited after-effects in the offspring of ultrasound pre-treated parental plants remains open as this has not yet been investigated before. As ultrasound treatment potentially mitigates drought stress-related adverse effects (yield loss) [16] therefore, the combined effect of ultrasound and drought pre-treatment on phenotypic plasticity was examined.

Pre-treatment with PEG in the parental generation (C-PEG), improved the stress tolerance of the offspring significantly in terms of both tuber number and tuber weight (C-PEG-PEG) compared to the treatment group that received PEG treatment for the first time in the second generation (C-C-PEG). A previous study has concluded, that had a contrary result to our research because there was no significant difference regarding tuber yield in the progeny between pre-treated (or primed) and control potato plants [20]. However, differences in experimental results may also arise from differences in experimental setups. Furthermore, parental US pre-treatment (US-C-PEG) improved the performance of the offspring in terms of tuber weight more than PEG pre-treatment (C-PEG-PEG). However, the US-PEG-PEG treatment produced the best yield, both in tuber number and weight, therefore performed better than the control group under normal (C-C-C) and stressed conditions (C-C-PEG). In the case of plant height, C-PEG and US-PEG pre-treatment improves stress tolerance by 35% and 57% (C-PEG-PEG compared to C-C-PEG and US-C-PEG compared to US-PEG-PEG, respectively). In the case of leaf number, the same two pre-treatments also had an improving, remedial effect, as the leaf number was the same as the normally irrigated control group (i.e. there was no significant difference between C-C-C, C-PEG-PEG and US-PEG-PEG treatment groups) (Figure 2., Figure 3.). The same two pre-treatments caused faster sprouting by approximately 50% compared to the absolute control group. Stolon formation occurred significantly earlier in the US-PEG-PEG pretreatment group than in the control group (Table 1.).

Conclusions

In conclusion, although drought itself (induced by PEG treatment) has a preparatory effect on the offspring (and therefore on the next year's yield) [21-22], this effect can be further enhanced when combined with ultrasound. Ultrasound has wide application possibilities in horticulture and agriculture as a mechano-priming technique based on the fact that it is also considered an abiotic stress factor for plants that induces stress-defense responses. Furthermore, acoustic stimuli can prepare plants for other abiotic or biotic environmental stressors thus making them more resilient in the future. Note, that while the utilization of ultrasound in agriculture is a promising methodology, its application efficiency is influenced by other factors, including the duration of its exposure, frequency, intensity and the developmental phase of the plants [16]. However, all things considered, implementation of ultrasound treatment in agriculture may offer a cost-effective alternative to current methodologies to address the adverse effects of climate change.

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