Maternal Environmental Effects of Temperature and Exogenous Gibberellic Acid on Seed and Seedling Traits of Four Populations of Evening Primrose (Oenothera biennis)

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Abstract: Earlier studies have considered the separate effects of temperature and gibberellic acid (GA3) on plants and seeds. However, the combined effects of these factors on parent plants and their progeny have received little attention. We investigated the effects of two temperature regimes (24/20 °C and 28/24 °C, 16 h light/8 h dark) and two GA3 treatments (for two weeks) on the reproductive yield of parent plants, the subsequent seed germinability, and the seedling traits of four local populations of evening primrose (Oenothera biennis). Mature seeds were harvested and germinated, and seedlings were grown under the two temperature regimes. Parent plants were phenotyped for flower area and diameter, capsule length and width, full and empty capsule masses, and seed number and mass per capsule. Additionally, seed total germination and germination rate were determined, alongside stem height and dry mass, leaf number, area and dry mass, root dry mass, and total dry mass in seedlings. GA3 promoted the flowering of all populations in the first year. Maturation drying under higher temperatures resulted in more viable and faster germinating seeds. Higher GA3 did not affect total germination, but increased the germination rate of seeds that produced seedlings with lower total dry mass under the higher temperature regime. In conclusion, all populations responded similarly to GA3 treatment in terms of flowering, but responded differently to temperature during seed maturation, and subsequent seed germination and seedling growth.

Keywords: evening primrose; gibberellic acid; Oenothera biennis; population; temperature; reproductive yield; seed germination; seedling growth

1. Introduction

Environmental factors, such as temperature, can affect the growth and reproductive yield of a parent plant and its progeny [1,2]. It is well documented that the parent plant has a significant effect on seed traits, including seed size, seed germination, and seedling growth [3–9]. During seed development and maturation drying, even one degree Celsius can have an important consequence for subsequent seed performance [10], potentially influencing seed quality traits, including dormancy. Dormancy is “regarded as the failure of an intact viable seed to complete germination under favorable conditions” [11], and the mechanisms by which it can be imposed by the parent plant or the parent environment remain unknown [2].

Maturation temperature alters seed germinability by affecting the metabolic activity of the parent plant and influencing the chemical constituents of seeds [12–15]. Earlier studies have examined the effects of single environmental factors (e.g., temperature, photoperiod, light quality, watering regime [1], and shading [16]) during seed development on subsequent germinability [1]. In many cases, higher maturation temperatures increased seed germination compared to lower maturation temperatures [2,6,7,17]. For example, in Scotch thistle (Onopordum acanthium), a high cypsela germinability was positively correlated with higher maturation temperatures [18,19].
Plant hormones are important in the regulation of plant growth and development [20]. Gibberellins are a large group of phytohormones that have many functions in plants, including stimulating stem elongation and inducing seed germination [21–24]. It has been shown that gibberellins, including GA₃, enhance flowering [25,26], shorten the time to flowering, increase the size and number of flowers [27,28], and promote subsequent plant growth and biomass production [29]. However, the effects of parent plant treatment with GA₃ on its progeny have not been fully understood.

Plant populations respond differently to abiotic factors [6,12]. Differences among populations can be related to non-genetic factors, such as the parent environment during seed maturation [30]. Although the separate effects of temperature and GA₃ have been studied on many plants [6], the interactive effects of these factors on parent plants and their progeny have not been addressed, especially in multiple local populations.

In this study, we selected evening primrose (*Oenothera biennis* L., Onagraceae). This plant species grows naturally across North America in ditches and waste areas with little shade on well-drained gravel soils [31]. It is also cultivated industrially for its linoleic acid and \( \gamma \)-linolenic acid, which are used for medicinal purposes [32,33]. The evening primrose seed oil extract contains 70–74% linoleic acid [33] and 8–10% \( \gamma \)-linolenic acid [33–36]. These fatty acids play a role in the proper functioning of human tissues because they serve as precursors of the anti-inflammatory eicosanoids [33].

Evening primrose naturally remains as vegetative rosettes in the first year of its life cycle, and after a period of overwintering becomes reproductive in the second year [31,37]. In the second year, plants bolt and grow up to 1.5 m in height, with yellow-colored flowers that are 3–4 cm in diameter [31]. Seed capsules that contain many seeds ripen and split open toward the end of the growing season (e.g., June–September, Halifax, Nova Scotia, Canada) to facilitate dispersal [38,39]. Seeds of evening primrose are dark brown with hard outer seed coats and are irregularly shaped [31], and exhibit an annual conditional dormancy–nondormancy cycle [6].

Previously, we have reported that the growth and physiological aspects of this species can be influenced by temperatures. In this study, it was shown that higher temperatures can increase stem height, photosynthetic pigments, and ethylene, but decrease gas exchange and, in turn, plant biomass [39]. Based on the earlier findings, we investigated the effects of temperature and GA₃ on the reproductive yields of the parent plants, the subsequent seed germinability, and the seedling traits of four populations of evening primrose. In the present study, the following hypotheses were tested: (i) higher temperatures decrease the reproductive yields of the parent plants, increase the subsequent germinability of seeds, and modify the subsequent seedling growth; (ii) GA₃ enhances the flowering of the parent plants regardless of its exogenous level, and increases subsequent seed germination and seedling height, and (iii) populations vary in their responses to temperature and exogenous GA₃.

### 2. Materials and Methods

#### 2.1. Plant Materials and Growth Conditions

Four local populations of evening primrose—Mainland Commons Baseball Field (MC), Radcliffe Drive (RD), Willet Street (WS) and Farnham Gate Road (FG); Halifax, Canada—were used. The soil pH of the seed collection sites was determined essentially as described in McLean [40] (see Table 1). From each population, ripe seeds were collected from ~15 plants, pooled together and germinated in 9 cm-diameter glass Petri dishes on one layer of blue germination filter paper (Anchor Paper Co., St. Paul, MN, USA) initially moistened with 10 mL of distilled water. More water was added each day as needed. For seven days, the seeds were incubated under a temperature regime of 24/20 °C (16 h light/8 h dark) and photosynthetic photon flux density (PPFD) of 300 \( \mu \)mol m\(^{-2}\) s\(^{-1}\) in a controlled environment growth chamber (Model ATC26, Conviron, Controlled Environments, Winnipeg, MB, Canada). Light in the growth chambers was provided with a mixture of cool white fluorescent tubes (Philips Master, TL-D-58W/840, Amsterdam, The Netherlands) and incandescent bulbs (Litemor, Boston, MA, USA). From each population, 10 seedlings were
randomly selected and transplanted into one-liter pots containing a mixture of peat moss, Perlite and Vermiculite (2:1:1, by volume), and approximately 30 pellets of slow-releasing fertilizer (NPK, 14-14-14; Type 100, Chisso-Asahi Fertilizer Co. Ltd., Tokyo, Japan) were added to each pot. The seedlings were placed in the same growth chamber for five days to acclimatize before placing them under two experimental temperature conditions (24/20 °C and 28/24 °C, 16 h light/8 h dark; relative humidity of ~65%). In both growth chambers, the PPFD was 300 µmol m⁻² s⁻¹. For the first 14 days in which the plants were under the experimental conditions, from each population, half of the plants were treated with 100 µL of 1 mg mL⁻¹ GA₃ solution every day (they received 1.4 mg GA₃ in total; higher level), and half of the plants were treated with 100 µL of 1 mg mL⁻¹ GA₃ solution every other day (they received 0.7 mg GA₃ in total; lower level). The plants were treated with GA₃ to promote flowering in their first year. A preliminary study revealed that, for such purpose, a two-week treatment with GA₃ was sufficient. Plants were grown to maturity, and after seven months ripe capsules were harvested for further studies.

| Population                  | Latitude and Longitude | Soil pH | Habitat                                      |
|-----------------------------|------------------------|---------|----------------------------------------------|
| Mainland Commons Baseball Field (MC) | 44.65993° N 63.66154° W | 7.6     | Open area with no shade, near a gravel path  |
| Radcliffe Drive (RD)        | 44.66602° N 63.65871° W | 5.9     | On the edge of woods with no shade, near a sidewalk |
| Willet Street (WS)          | 44.65791° N 63.65408° W | 6.2     | On the edge of a gravel driveway with no shade |
| Farnham Gate Road (FG)      | 44.67212° N 63.67111° W | 6.4     | On the edge of a walking path with no shade |

2.2. Measurement of Morphological Traits of Flowers, Capsules and Seeds

From each treatment, three fully-open flowers were randomly selected and detached; their diameter was measured with a ruler, and their area with an area meter (Delta-T Devices, Ltd., Cambridge, UK). Later, from each treatment, nine ripe capsules were harvested and placed in coin envelopes. Then, capsule length was measured with a standard millimeter ruler and capsule width with a Digimatic caliper (Mitutoyo Corp., Kanagawa, Japan). Capsule mass (full and empty) was measured with an analytical balance (Model ED224s, Sartorius, Goettingen, Germany). After that, from the selected capsules, seeds were extracted and counted, and their mass was determined.

2.3. Measurement of Total Germination and Germination Rate of Seeds

In each treatment, three replications of 50 seeds were germinated in Petri dishes in growth chambers under two temperature regimes (24/20 °C and 28/24 °C; 16 h light/8 h dark). Germinated seeds (radicle of 2 mm or longer) were counted and removed daily. Petri dishes were arranged randomly in the chamber at the start of the experiment and replaced in different random patterns after each germination count. The experiment was terminated after five consecutive days with no germination (typically after 30 days). At the end, non-germinated seeds were subjected to a viability test using a 1% (w/v) solution of tetrazolium chloride [41], and the total germination percentage and germination rate were determined [42].

2.4. Measurement of Morphological Traits of Seedlings

Under each treatment, seeds were germinated in Petri dishes for seven days; then, 10 seedlings from each treatment were transplanted into pots, following the above-described procedure. After being acclimatized for five days at 24/20 °C (16 h light/8 h dark), the seedlings were grown at 24/20 °C and 28/24 °C (16 h light/8 h dark) for three weeks. On day 21, the stem height was measured first for three randomly selected plants, and then
from each treatment, three plants were harvested to determine the dry masses of individual plant parts (leaf, stem and root). After weighing the fresh mass of plant samples with an analytical balance, they were dried at 60 °C for 72 h in a forced-air Fisher Isotemp Premium oven (Model 750F, Fisher Scientific, Nepean, Ontario, Canada), and reweighed with the same balance. Leaf area was measured with the area meter.

2.5. Data Analysis

Data for flower, capsule and seed traits, seed total germination and germination rate, and seedling traits were analyzed separately by means of analysis of variance (ANOVA) to determine the effects of population, maturation temperature, seedling temperature, and GA$_3$ level. A three-way ANOVA was used for flower, capsule and seed traits, and a four-way ANOVA for seed germination and seedling traits [43]. Data were subjected to Levene’s test of homogeneity of variance, and for seed germination, they were transformed to the arcsine square root of percentage to normalize the variance [44]. A Scheffé’s test was used to determine differences among the treatments of each plant trait at the 5% level [43].

The coefficient of germination rate (CGR) was calculated for each replicate according to the following equation: $\text{CGR} = N/\sum n_i d_i$, where $N$ is the total germination, $n_i$ is the number of germinated seeds on the particular day on which a count was made, and $d_i$ is the number of days from the start of the experiment [45]. All values of CGR are between 0 (no germination) and 1 (fastest germination rate) [42]. Additionally, the relationship between plant/seed traits was determined for each treatment by the Pearson’s correlation coefficient [46]. All data are reported as mean ± standard error.

3. Results

3.1. Morphological Traits of Flowers, Capsules and Seeds

In this study, the MC and FG populations produced flowers with the largest area and diameter, whereas the WS population produced flowers with the smallest area and diameter. The RD population was in between these two categories in terms of flower size (Figure 1A,D). Flower area and diameter were significantly affected by population, the two-way interactions of P (population) × M (maturation temperature) and M × G (plant treatment of GA$_3$), and the three-way interaction of these factors. Flower diameter was also affected by P × G (Table 2). On the basis of the three-way interaction, flower area and diameter were largest in plants of the MC population, treated with a higher GA$_3$ level and grown under a lower temperature regime (area: 15.04 ± 1.77 cm$^2$; diameter: 5.33 ± 0.32 cm), but smallest in the plants of the WS population, treated with the same GA$_3$ level and grown under the higher temperature regime (area: 1.69 ± 0.06 cm$^2$; diameter: 1.87 ± 0.03 cm).

Capsules were longest in the MC population, but shortest in the RD and FG populations (Figure 1G). Capsules from the MC and WS populations had 9 and 12% greater widths, respectively, than capsules from the RD population (Figure 1J). Full and empty capsule masses were highest in the MC population, but lowest in the WS population (Figure 1M,P). Higher maturation temperatures decreased capsule length, width, full mass, and empty mass, compared to the lower maturation temperatures (Figure 1H,K,N,Q). The capsule width was 5% higher in plants that were treated with lower GA$_3$ levels than in plants that were treated with higher GA$_3$ levels (Figure 1L). Capsule length, width, full mass and empty mass were significantly affected by P, M, and the two-way interaction of P × M. Capsule width and empty mass were also affected by P × G. Capsule width, full mass and empty mass were significantly affected by the three-way interaction of these factors (Table 2). Maturation temperature had different influences on the capsule length across populations, as the MC population produced the longest capsules under the lower temperature regime (25.33 ± 0.86 mm), whereas the FG population produced the shortest capsules under the higher temperature regime (15.00 ± 0.52 mm). Based on the three-way interaction, the capsules with the greatest width were produced on plants of the WS population, treated with a lower GA$_3$ level and grown under the lower temperature regime.
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(5.43 ± 0.11 mm), but capsules with the smallest width were produced on plants of the same population, with the same GA₃ treatment and grown under the higher temperature regime (3.70 ± 0.17 mm). On the basis of the three-way interaction, the MC population that was grown at lower temperatures and treated with higher GA₃ levels had the heaviest full capsules (992.50 ± 34.94 mg), whereas the WS population that was grown at higher temperatures and treated with lower GA₃ levels had the lightest full capsules (667.62 ± 3.46 mg). The three-way interaction also revealed that the MC population, which was grown at lower temperatures and treated with a higher GA₃ level, had the heaviest empty capsules (850.52 ± 35.20 mg), and the WS population, which was grown at lower temperatures and treated with lower GA₃ levels, had the lightest empty capsules (617.57 ± 1.44 mg).

Figure 1. Effects of population, maturation temperature and gibberellic acid (GA₃) on flower, capsule and seed traits of evening primrose (Oenothera biennis). Flowers, capsules and seeds were produced by the parent plants of four populations, which were treated with two GA₃ levels (0.7 and 1.4 mg), and grown for seven months under two temperature regimes (24/20 °C and 28/24 °C; 16 h light, 8 h dark) in controlled environment growth chambers. (A–C), flower area; (D–F), flower diameter; (G–I), capsule length; (J–L), capsule width; (M–O), full capsule mass; (P–R), empty capsule mass; (S–U), seed number per capsule; (V–X), seed mass per capsule; (A, D, G, J, M, P, S, V), population; (B, E, H, K, N, Q, T, W), maturation temperature; and (C, F, J, L, O, R, U, X), gibberellic acid. The data are means ± SE of three biological replications for flower and nine replications for capsule and seed. Bars with different letters within each panel are significantly different (p < 0.05) according to Scheffé’s test. MC, Mainland Commons Baseball Field; RD, Radcliffe Drive; WS, Willet Street; FG, Farnham Gate Road.
Table 2. Analysis of variance (F value) for population, maturation temperature, gibberellic acid, and their interactive effects on the reproductive yield of evening primrose (*Oenothera biennis*). Flowers, capsules and seeds were produced by the parent plants of four populations, which were treated with two GA3 levels (0.7 and 1.4 mg), and grown for seven months under two temperature regimes (24/20°C and 28/24°C; 16 h light, 8 h dark) in controlled environment growth chambers. Significance values: * p < 0.05; ** p < 0.01; *** p < 0.001; **** p < 0.0001.

| Source                     | Flower (Capsule) | Seed (Capsule −1) |
|----------------------------|------------------|-------------------|
|                            | Area             | Diameter          | Length | Width | Full Mass | Empty Mass | Number | Mass     |
| Population (P)             | 99.53 ****       | 139.39 ****       | 34.31 **** | 6.54 *** | 85.04 **** | 81.12 **** | 19.57 **** | 29.32 **** |
| Maturation temperature (M) | 0.16             | 0.24              | 74.11 **** | 27.75 **** | 9.90 **    | 34.14 **** | 0.22    | 0.44     |
| Gibberellic acid (G)       | 1.93             | 1.94              | 1.38    | 6.87 ** | 1.03       | 2.90       | 1.25    | 0.00     |
| P × M                     | 4.53 **          | 12.07 ****        | 9.94 **** | 14.18 **** | 10.05 **** | 16.32 **** | 12.67 **** | 4.74 **   |
| P × G                     | 1.77             | 3.33 *            | 1.25    | 5.56 ** | 1.67       | 5.57 **    | 0.89    | 0.77     |
| M × G                     | 17.62 ***        | 13.59 ****        | 1.54    | 0.80    | 0.86       | 1.62       | 1.79    | 6.24 *    |
| P × M × G                 | 20.48 ****       | 27.28 ****        | 1.81    | 3.09 *  | 7.04 ****  | 9.65 ****  | 1.01    | 5.02 **   |

The MC population produced the highest number and mass of seeds per capsule, whereas the WS population produced the lowest number and mass of seeds per capsule (Figure 1S,V). Seed number and mass were significantly affected by P and the two-way interaction of P × M. Seed mass was also affected by the two-way interaction of M × G, and the three-way interaction of these factors (Table 2). The two-way interaction of P × M revealed that the MC population, grown under lower temperatures, produced the greatest number of seeds (148.39 ± 17.54 capsule −1), whereas the WS population, grown under higher temperatures, produced the lowest number of seeds (39.11 ± 1.71 capsule −1). On the basis of the three-way interaction, total seed mass was highest in the MC population that was grown under the lower temperature regime and treated with lower GA3 levels (163.98 ± 8.81 mg capsule −1), but it was lowest in the WS population that was grown under the higher temperature regime and had the same GA3 treatment (47.52 ± 3.27 mg capsule −1).

3.2. Total Germination and Germination Rate of Seeds

The RD and WS populations produced seeds with at least 15% higher total germination than the MC and FG populations (Figure 2A). Additionally, seeds that matured under the higher temperature regime showed 11% higher total germination than seeds that matured under the lower temperature regime (Figure 2C). Seed total germination was significantly affected by P, M, the two-way interaction of P × I, the three-way interactions of P × I × M, P × M × G, and I × M × G, and the four-way interaction of these factors (Table 3). Based on the four-way interaction, seeds of the WS population (treated with higher GA3 level) that matured at higher temperatures and were incubated at lower temperatures had the highest total germination (77.84 ± 2.02), whereas seeds of the MC population (treated with lower GA3 level) that matured at lower temperatures and incubated at lower temperatures had the lowest total germination (43.04 ± 3.82). All non-germinated seeds were viable.

The WD population produced seeds with the fastest germination rate, whereas the FG population produced seeds with the slowest germination rate. The RD and MC populations showed the second and third lowest germination rates, respectively (Figure 2E). Seeds that matured under higher temperatures showed faster germination rates than seeds that matured under lower temperatures, as was similar to total germination (Figure 2G). Seed germination rate was significantly affected by P, M, G, the two-way interactions of P × I, P × M, and P × G, the three-way interactions of P × I × M, P × I × G, and I × M × G, and the four-way interaction of these factors (Table 3). On the basis of the four-way interaction, seeds of the WD population (treated with higher GA3 level) that matured at higher temperatures and were incubated under higher temperatures had the fastest germination rate (39.42 ± 4.96), whereas seeds of the FG population (treated with higher...
GA₃ level) that matured under higher temperatures and were incubated under lower temperatures had the slowest germination rate (5.18 ± 3.46).

**Figure 2.** Effects of population, incubation temperature, maturation temperature and gibberellic acid (GA₃) on seed germination and rate of evening primrose (*Oenothera biennis*). Seeds were matured on the parent plants of four populations, which were treated with two GA₃ levels (0.7 and 1.4 mg), grown for seven months under two temperature regimes (24/20 °C and 28/24 °C; 16 h light, 8 h dark), and incubated under the above temperature regimes for 30 days in controlled environment growth chambers. (A–D), germination percentage; (E–H), germination rate; (A,E), population; (B,F), incubation temperature; (C,G), maturation temperature; and (D,H), gibberellic acid. The data are means ± SE of the three biological replications. Bars with different letters within each panel are significantly different (p < 0.05) according to Scheffe’s test. MC, Mainland Commons Baseball Field; RD, Radcliffe Drive; WS, Willet Street; FG, Farnham Gate Road.

**Table 2.** Analysis of variance (F value) for population, maturation temperature, incubation temperature, and their interactive effects on seed germination and rate of evening primrose (*Oenothera biennis*). Seeds matured on the parent plants of four populations, which were treated with two GA₃ levels (0.7 and 1.4 mg), grown for seven months under two temperature regimes (24/20 °C and 28/24 °C; 16 h light, 8 h dark) and incubated under the above temperature regimes for 30 days in controlled environment growth chambers. From each treatment, three replications of 50 seeds were germinated. Significance values: * p < 0.05; ** p < 0.01; **** p < 0.0001.

| Source                     | Seed Total Germination | Seed Germinate Rate |
|----------------------------|------------------------|---------------------|
| Population (P)             | 31.55 ****             | 192.89 ****         |
| Incubation temperature (I) | 0.50                   | 2.18                |
| Maturation temperature (M) | 31.72 ****             | 58.66 ****          |
| Gibberellic acid (G)       | 1.04                   | 4.49 *              |
| P × I                      | 1.74                   | 22.94 ****          |
| P × M                      | 1.66                   | 4.67 **             |
| P × G                      | 0.54                   | 3.96 *              |
| I × M                      | 5.02 *                 | 0.00                |
| I × G                      | 1.72                   | 2.06                |
| M × G                      | 0.01                   | 1.24                |
| P × I × M                  | 5.81 **                | 12.56 ****          |
| P × I × G                  | 0.26                   | 3.74 *              |
| P × M × G                  | 3.12 *                 | 1.94                |
| I × M × G                  | 25.26 ****             | 8.59 **             |
| P × I × M × G              | 2.95 *                 | 3.96 *              |
3.3. Morphological Traits of Seedlings

In the seedlings, the MC population had taller stems than the other populations. Seedlings that were grown under the higher temperature regime were taller than those grown under the lower temperature regime. Seeds that had matured under higher temperatures produced taller seedlings than seeds that had matured under lower temperatures (Table 4). Additionally, seeds that matured on plants that were treated with higher GA$_3$ levels produced taller seedlings than those from seeds that matured on plants that were treated with lower GA$_3$ levels (Table 4). The stem height was significantly affected by P, S (seedling temperature), M, G, the two-way interactions of P x S, P x M, P x G, and M x G, all three-way interactions, and the four-way interaction of these factors (Table 5). On the basis of the four-way interaction, seeds of the MC population (treated with lower GA$_3$ level) that matured under higher temperatures and were grown under higher temperatures produced the tallest seedlings (8.94 ± 0.07 cm), whereas seeds of the RD population (treated with lower GA$_3$ level) that matured at lower temperatures and were grown under higher temperatures produced the shortest seedlings (3.88 ± 0.36 cm).

The MC population produced seedlings that had the highest leaf number, whereas the FG population produced seedlings that had the lowest leaf number (Table 4). Higher temperatures caused seedlings to have 12% fewer leaves than lower temperatures. The seedlings that originated from seeds of plants that were treated with higher GA$_3$ levels produced 6% more leaves than the seedlings that originated from seeds of plants that were treated with lower GA$_3$ levels (Table 4). Leaf number was significantly affected by P, S, G, the two-way interactions of P x S, P x M, P x G, and M x G, and the three-way interactions of P x S x M, and P x S x G (Table 5). Based on the two- and three-way interactions, the seedlings of the MC population (treated with higher GA$_3$ level) that matured under higher temperatures and were grown under lower temperatures produced the highest number of leaves (15.00 ± 0.58), whereas seedlings of the FG population (treated with lower GA$_3$ level) that matured under higher temperatures and were grown under higher temperatures produced the lowest number of leaves (5.67 ± 0.33).

The FG population produced seedlings with larger leaves than other populations. Seedlings that were grown under higher temperatures had smaller leaves than seedlings that were grown under lower temperatures. Seeds that had matured under higher temperatures produced seedlings with larger leaves than seeds that had matured under lower temperatures (Table 4). Seedlings that originated from seeds of plants that were treated with higher GA$_3$ levels produced smaller leaves than seedlings that originated from seeds of plants that were treated with lower GA$_3$ levels (Table 4). Leaf area was significantly affected by P, S, M, G, the two-way interactions of P x S, P x M, P x G, and M x G, the three-way interaction of P x S x G, and the four-way interaction of these factors (Table 5). On the basis of the four-way interaction, seedlings of the FG population (treated with lower GA$_3$ level) that originated from seeds that matured under lower temperatures and were grown under lower temperatures produced the largest leaves (103.91 ± 0.16 cm$^2$ plant$^{-1}$), whereas seedlings of the WS population (treated with higher GA$_3$ levels) that originated from seeds that matured under lower temperatures and were grown under lower temperatures produced the smallest leaves (24.35 ± 0.36 cm$^2$ plant$^{-1}$).

The FG population had the highest leaf dry mass, whereas the WS population had the lowest leaf dry mass (Table 4). Leaf dry mass was 20% lower for seedlings that were grown under higher temperatures than seedlings that were grown under lower temperatures. The seedlings that originated from seeds that had matured under higher temperatures had 16% higher leaf dry mass than the seedlings that originated from seeds that had matured under lower temperatures (Table 4). Leaf dry mass was significantly affected by P, S, M, the two-way interactions of P x S, P x M, P x G, S x M, and M x G, and the three-way interactions of P x S x M, and P x S x G (Table 5). Based on the two- and three-way interactions, the seedlings of the FG population (treated with lower GA$_3$ level) that originated from seeds that matured under lower temperatures and were grown under lower temperatures produced the heaviest leaves (481.17 ± 89.63 mg plant$^{-1}$), whereas seedlings of the WS
population (treated with higher GA$_3$ level) that originated from seeds that matured under lower temperatures and were grown under lower temperatures produced the lightest leaves (72.50 ± 16.05 mg plant$^{-1}$).

Seeds that had matured under higher temperatures produced seedlings with 23% higher stem dry mass than seeds that had matured under lower temperatures (Table 4). Stem dry mass was significantly affected by M, G, the two-way interactions of P x S, P x M, S x M, and M x G, all three-way interactions, and the four-way interaction of these factors (Table 5). On the basis of the four-way interaction, seedlings of the MC population (treated with lower GA$_3$ level) that originated from seeds that matured under higher temperatures and were grown under higher temperatures had the highest stem mass (12.17 ± 0.90 mg plant$^{-1}$), whereas seedlings of the FG population (treated with lower GA$_3$ level) that originated from seeds that matured under higher temperatures and were grown under higher temperatures had the lowest stem mass (2.47 ± 0.26 mg plant$^{-1}$).

The MC population produced at least 37% higher root dry mass than the other populations. The root dry mass of seedlings was 31% lower under higher temperatures than under lower temperatures (Table 4). Root dry mass was significantly affected by P, S, the two-way interactions of P x S and M x G, and the three-way interaction of P x S x M (Table 5). Based on the two-way interactions of P x S and M x G, and the three-way interaction of P x S x M, seedlings of the MC population (treated with higher GA$_3$ level) that originated from seeds that matured under higher temperatures and were grown under lower temperatures had the highest root mass (417.00 ± 109.35 mg plant$^{-1}$), whereas seedlings of the FG population (treated with higher GA$_3$ level) that originated from seeds that matured under higher temperatures and were grown under lower temperatures had the lowest root mass (15.37 ± 1.59 mg plant$^{-1}$).

Additionally, the MC population produced at least 28% higher total dry mass than the other populations. Seedlings had 24% lower total dry mass under higher temperatures than under lower temperatures (Table 4). The seedling total dry mass was significantly affected by P, S, M, the two-way interactions of P x S, P x M, and M x G, and the three-way interactions of P x S x M, and P x S x G (Table 5). On the basis of two- and three-way interactions, seedlings of the MC population (treated with higher GA$_3$ level) that originated from seeds that matured under higher temperatures and were grown under lower temperatures had the highest total dry mass (825.37 ± 106.95 mg plant$^{-1}$), whereas seedlings of the WS population (treated with higher GA$_3$ level) that originated from seeds that matured under lower temperatures and were grown under lower temperatures had the lowest total dry mass (131.40 ± 19.00 mg plant$^{-1}$).

Relationship between Plant/Seed Traits

Pearson’s correlation analysis revealed significant (p < 0.05) relationships between plant/seed traits (Table 6). In the parent plants, flower area was positively correlated with flower diameter ($r = 0.993$). Capsule length was positively correlated with capsule width ($r = 0.506$). Full capsule mass was positively correlated with seed number per capsule ($r = 0.799$), and seed mass per capsule ($r = 0.866$). Seed mass per capsule was positively correlated with seed number per capsule ($r = 0.896$). In seed germination, the coefficient of germination rate was positively correlated with total germination ($r = 0.835$). In the subsequent seedlings, stem dry mass was positively correlated with seedling height ($r = 0.621$). Root dry mass and total dry mass per plant were positively correlated with leaf number per plant ($r = 0.640$ and $r = 0.647$, respectively). Leaf dry mass and total dry mass per plant were positively correlated with leaf area per plant ($r = 0.839$ and $r = 0.509$, respectively). Stem dry mass and total dry mass per plant were positively correlated with leaf dry mass per plant ($r = 0.547$ and $r = 0.742$, respectively). A positive relationship was found between total dry mass per plant and stem dry mass per plant ($r = 0.527$) and root dry mass per plant ($r = 0.882$).
Table 4. Effects of population, temperature of the seedling environment (seedling temperature), temperature of the parent environment (maturation temperature) and gibberellic acid (GA$_3$) treatment of the parent plant on seedling traits of evening primrose (Oenothera biennis). Seedlings were grown for three weeks under two temperature regimes (24/20°C and 28/24°C; 16 h light, 8 h dark) from seeds that matured on the parent plants of four populations, which were treated with two GA$_3$ levels (0.7 and 1.4 mg), in controlled environment growth chambers. The data are means ± SE of three biological replications. Means followed by different letters within each trait and factor are significantly different ($p < 0.05$) according to Scheffé’s test. MC, Mainland Commons Baseball Field; RD, Radcliffe Drive; WS, Willet Street; FG, Farnham Gate Road.

| Trait                        | Population | Seedling Temperature | Maturation Temperature | Gibberellic Acid Level |
|------------------------------|------------|----------------------|------------------------|-----------------------|
|                              | MC         | RD                   | WS                     | FG                    |
| Stem height (cm)             | 6.35 ± 0.30 a | 5.68 ± 0.31 b | 5.49 ± 0.16 b | 5.67 ± 0.16 b |
| Leaf number (plant$^{-1}$)   | 12.13 ± 0.34 a | 8.79 ± 0.41 b | 8.54 ± 0.26 b | 7.38 ± 0.40 c |
| Leaf area (cm$^2$ plant$^{-1}$) | 51.15 ± 3.49 b | 48.06 ± 2.18 b | 52.11 ± 3.43 b | 61.07 ± 4.15 a |
| Leaf dry mass (mg plant$^{-1}$) | 253.55 ± 20.79 ab | 210.92 ± 11.76 bc | 199.47 ± 14.60 c | 257.60 ± 27.93 a |
| Stem dry mass (mg plant$^{-1}$) | 6.06 ± 0.66 a | 5.58 ± 0.38 a | 5.36 ± 0.44 a | 5.35 ± 0.50 a |
| Root dry mass (mg plant$^{-1}$) | 213.63 ± 38.06 a | 73.03 ± 10.01 b | 132.94 ± 23.88 b | 72.52 ± 12.66 a |
| Total dry mass (mg plant$^{-1}$) | 473.23 ± 50.13 a | 289.52 ± 15.58 b | 337.75 ± 29.89 b | 335.43 ± 33.37 b |

Table 5. Analysis of variance ($F$ value) for population, temperature of the seedling environment (seedling temperature), temperature of the parent environment (maturation temperature), gibberellic acid (GA$_3$) treatment of the parent plant, and their interactive effects on seedling traits of evening primrose (Oenothera biennis). Seedlings were grown for three weeks under two temperature regimes (24/20°C and 28/24°C; 16 h light, 8 h dark) from seeds that matured on the parent plants of four populations, which were treated with two GA$_3$ levels (0.7 and 1.4 mg), in controlled environment growth chambers. From each treatment, three replications of seedlings were measured. Significance values: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$.

| Source          | Stem Height | Leaf Number | Leaf Area | Leaf Dry Mass | Stem Dry Mass | Root Dry Mass | Total Dry Mass |
|-----------------|-------------|-------------|-----------|---------------|---------------|---------------|----------------|
| Population (P)  | 13.87 ****  | 81.27 ****  | 13.20 **** | 6.98 ***      | 1.36          | 13.06 ****    | 10.37 ****     |
| Seedling temperature (S) | 14.22 ***  | 26.58 ****  | 6.24 *    | 20.77 ****    | 0.00          | 6.13 *        | 15.30 ***      |
| Maturation temperature (M) | 44.17 **** | 0.31        | 8.32 **   | 13.59 ***     | 25.22 ****    | 2.07          | 7.89 **        |
| Gibberellic acid (G) | 16.02 ***  | 5.73 *      | 5.04 *    | 1.35          | 1.68          | 1.00          | 1.59           |
| P × S           | 23.51 ****  | 6.28 **     | 31.07 **** | 15.39 ***     | 28.09 ****    | 4.59 **       | 4.93 **        |
| P × M           | 16.18 ****  | 9.62 ****   | 36.86 **** | 9.61 ****     | 4.11 **       | 1.59          | 4.90 **        |
| P × G           | 34.73 ****  | 4.64 **     | 17.21 **** | 10.24 ****    | 2.36          | 2.19          | 2.30           |
| S × M           | 0.54        | 1.66        | 0.21      | 7.69 **       | 11.85 **      | 3.72          | 0.02           |
Table 5. Cont.

| Source            | Stem Height | Leaf Number | Leaf Area | Leaf Dry Mass | Stem Dry Mass | Root Dry Mass | Total Dry Mass |
|-------------------|-------------|-------------|-----------|---------------|---------------|---------------|----------------|
| S × G             | 0.62        | 0.31        | 1.00      | 0.73          | 3.63          | 0.82          | 0.10           |
| M × G             | 4.79 *      | 6.64 *      | 23.95 **** | 8.74 **       | 4.27 *        | 21.32 ****    | 23.28 ****     |
| P × S × M         | 13.76 ****  | 2.84 *      | 2.18      | 7.03 ***      | 9.22 ****     | 4.12 **       | 4.08 *         |
| P × S × G         | 8.22 ***    | 11.97 ****  | 7.16 ***  | 12.99 ****    | 3.30 *        | 1.78          | 3.81 *         |
| S × M × G         | 7.21 **     | 3.39        | 3.23      | 0.33          | 6.69 *        | 0.78          | 0.18           |
| P × S × M × G     | 13.29 ****  | 2.21        | 8.41 **** | 0.86          | 4.08 **       | 1.84          | 1.32           |

Table 6. Pearson’s correlation coefficient between reproductive traits of the parent plant, subsequent seed total germination, germination rate, and seedling traits of evening primrose (*Oenothera biennis*). Flowers, capsules and seeds were produced by the parent plants of four populations, which were treated with two gibberellic acid (GA₃) levels (0.7 and 1.4 mg), and grown for seven months under two temperature regimes (24/20 °C and 28/24 °C; 16 h light, 8 h dark) in controlled environment growth chambers. Fresh mature seeds were incubated for 30 days, and seedlings were grown for three weeks under the same temperature regimes. Significance values: * p < 0.05; ** p < 0.01; *** p < 0.001.

| Trait                     | 1   | 2         | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   | 11   | 12   | 13   | 14   | 15   | 16   |
|---------------------------|-----|-----------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Flower area               | -   |           |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Flower diameter           | 0.993 *** |          |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Capsule length            | 0.184 | 0.196     |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Capsule width             | 0.300 | 0.279     | 0.506 * |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Full capsule mass         | 0.150 | 0.127     | 0.427 | 0.044 |      |      |      |      |      |      |      |      |      |      |      |      |
| Empty capsule mass        | 0.087 | 0.080     | 0.449 | 0.042 | 0.947 *** |      |      |      |      |      |      |      |      |      |      |
| Seed number capsule⁻¹     | 0.396 | 0.355     | 0.367 | 0.184 | 0.799 *** | 0.625 * |      |      |      |      |      |      |      |      |      |
| Seed mass capsule⁻¹       | 0.215 | 0.173     | 0.299 | 0.169 | 0.866 *** | 0.658 ** | 0.896 *** |      |      |      |      |      |      |      |      |
| Total germination         | 0.230 | 0.271     | –0.328 | –0.156 | –0.619 * | –0.633 ** | –0.505 * | –0.463 |      |      |      |      |      |      |      |      |
| Germination rate          | 0.211 | 0.265     | –0.003 | –0.137 | –0.591 * | –0.535 ** | –0.573 * | –0.551 * | 0.835 *** |      |      |      |      |      |      |
| Seedling stem height      | 0.094 | 0.088     | –0.089 | 0.056 | 0.214 | 0.135 | 0.205 | 0.290 | 0.055 | –0.038 |      |      |      |      |      |
| Leaf number plant¹        | –0.065 | –0.054    | 0.412 | 0.031 | 0.551 * | 0.545 * | 0.221 | 0.441 | –0.164 | 0.025 | 0.454 |      |      |      |      |
| Leaf area plant⁻¹         | –0.543 * | –0.540 * | –0.324 | –0.047 | –0.152 | –0.167 | –0.227 | –0.096 | –0.171 | –0.216 | 0.374 | 0.093 |      |      |      |
| Leaf dry mass plant⁻¹     | –0.383 | –0.387    | –0.376 | –0.209 | 0.136 | 0.100 | –0.033 | 0.162 | –0.242 | –0.306 | 0.440 | 0.379 | 0.839 *** |      |      |
| Stem dry mass plant⁻¹     | 0.114 | 0.100     | –0.399 | –0.126 | –0.004 | –0.061 | –0.050 | 0.085 | 0.229 | 0.119 | 0.621 * | 0.398 | 0.446 | 0.547 * |      |
| Root dry mass plant⁻¹     | 0.127 | 0.124     | 0.353 | 0.068 | 0.214 | 0.121 | 0.207 | 0.311 | –0.127 | 0.164 | 0.170 | 0.640 ** | 0.126 | 0.339 | 0.345 |      |
| Total dry mass plant⁻¹    | –0.098 | –0.103    | 0.060 | –0.056 | 0.219 | 0.135 | 0.130 | 0.302 | –0.207 | –0.033 | 0.345 | 0.647 ** | 0.509 * | 0.742 ** | 0.527 * | 0.882 *** |
4. Discussion

In this study, for the first time, we have investigated the effects of temperature on the seed maturation, seed germination and seedling growth of progenies that originated from parent plants that were treated with GA$_3$. In four populations, eight traits were considered for reproductive yield, two traits for seed germination, and seven traits for seedling growth. Overall, differences between/among treatments were significant in 113 cases (Tables 2, 3 and 5).

4.1. Interacting Factors Regulate the Morphological Traits of Reproductive Yield

Overall, the populations of evening primrose produced flowers of different sizes (Table 2). The flowers were largest in the MC population that was treated with a higher GA$_3$ level and grown under lower temperatures, but smallest in the WS population that was treated with a higher GA$_3$ level and grown under higher temperatures (Figure 1). In these two populations, the different flower sizes indicate that temperature, but not GA$_3$, plays a major role in flower setting in this species. An earlier study has also shown an inverse relationship between temperature and flower size [47]. Similar trends were also found for the full and empty capsule masses among populations (Table 2). Lower temperatures caused the parent plants of the MC population to produce more seeds per capsule, whereas higher temperatures led plants of the WS population to produce fewer seeds per capsule. This indicates that the populations of evening primrose respond differently to temperature, and higher maturation temperature decreases seed number per capsule, confirming previous findings in other plant species [6,19]. However, GA$_3$ modified the above patterns for the total seed mass, as plants of the MC population that were grown under lower temperatures and treated with a lower GA$_3$ level had the highest seed mass, whereas plants of the WS population that were grown under higher temperatures and treated with lower GA$_3$ level had the lowest seed mass (Figure 1). Pinthus et al. [48] noted that plants are more responsive to GA$_3$ under lower temperatures. Our study showed that, although the individual factors, i.e., population, maturation temperature and GA$_3$, may not affect some reproductive yield traits (e.g., flower area and diameter), interactions among the main factors modify the ultimate outcome (Table 2). Earlier studies have shown that the parental environment can affect various aspects of seeds, including size and chemical composition [1,6,17], and temperature is one of the most frequently studied environmental factors in this respect [18,49,50]. For example, higher maturation temperatures reduced the seed mass of the narrow-leaved plantain (Plantago lanceolata) [3].

4.2. Maturation Temperature Exerts Major Effects on Subsequent Seed Performance

The germination patterns were different among populations (Table 3), and were somewhat opposite to those of the reproductive yield traits (i.e., seed mass). Plants that were grown under higher temperatures produced more germinable seeds than those grown under lower temperatures. Other plant species have also exhibited such patterns [1,6,19,30]. For example, seeds of groundsel (Senecio vulgaris) that matured at 22/10 °C had a higher total germination than those that matured at 15/8 °C [51]. In mouse-ear cress (Arabidopsis thaliana), seeds that matured at 28/24 °C were more germinable than seeds that matured at 22/18 °C [52]. In these species, it is likely that the higher temperature inhibits the ability of plants to accumulate compounds, such as abscisic acid, that play a role in the induction of seed dormancy [6,11,53]. In our study, the total germination was highest in seeds of the WS population that were treated with lower GA$_3$ levels and grown at higher temperatures, but lowest in the seeds of the MC population that were treated with lower GA$_3$ levels and grown under lower temperatures (Figure 2). Germination rate showed similar pattern to that of total germination in terms of variation among populations (Table 3). Seeds of the WS population that matured on plants that were treated with higher GA$_3$ levels, grown under higher temperatures, and incubated under higher temperatures had the fastest germination rate, whereas seeds of the FG population that matured on plants that were treated with higher GA$_3$ levels, grown under higher temperatures, and incubated under lower temperatures had the slowest germination rate. The other two pop-
ulations (MC and RD) also had slower germination rates than the WS population (Figure 2). Although the seeds were not responsive to incubation temperatures, as an individual factor, they were indeed responsive to the interactive effects of population, incubation temperature, maturation temperature, and GA$_3$ (Table 3). Because these seeds originated from populations that were grown under the same controlled environment conditions, differences in their performance likely have a genetic basis, as shown in seeds of other plant species [30,54]. In our study, higher temperatures during seed maturation increased seed germinability, which is similar to earlier findings in this species [6], as well as in some other species, such as narrow-leaved plantain [3] and Scotch thistle [19]. However, they differ from some other findings, such as in stinkweed (Thlaspi arvense) [55] and night-flowering catchfly (Silene noctiflora) [56], in which increased parental growth temperature decreased subsequent seed germination. In general, a strong positive relationship was found between the total germination and germination rates of seeds (Table 6). Overall, populations that positively respond to higher temperatures during seed maturation and subsequent germination will undergo more complete and faster germination than populations that are less responsive to increased atmospheric temperatures.

4.3. Parent Environment Modifies Morphological Traits of Subsequent Seedlings

Except for the stem dry mass, populations varied in seedling traits (Table 5). Plants from the MC population grew tallest, had the most leaves, and produced the highest root and total dry masses. However, plants from the WS population grew shortest, and had the lowest leaf dry mass, and plants from the FG population produced the fewest, but the largest and heaviest, leaves. On the other hand, plants from the RD population produced the smallest leaves, and had the lowest total dry mass (Table 4). It seems that the largest seeds of the MC population gave rise to the largest seedlings (Figure 1; Table 4), confirming earlier reports in this species [6]. The interpopulation variation could be related to environmental or genetic factors, or a combination of both [57]. During seedling growth, the higher temperature regime increased seedling height. Additionally, seedlings under the higher temperature regime had fewer, smaller and lighter leaves, as well as lighter root and total dry masses, than seedlings under the lower temperature regime. The adverse effect of high temperatures on plant biomass has already been reported in other species [58]. Higher temperatures during seed development led to seedlings that were taller with larger and heavier leaves, as well as with heavier stem and total dry masses, than at lower temperatures. Seedlings that originated from seeds of parent plants that were treated with higher GA$_3$ levels were taller and produced smaller leaves than seedlings that originated from seeds of the parent plants that were treated with lower GA$_3$ levels (Table 4). This may indicate the influence of the parent plant’s hormonal properties (e.g., GA$_3$) on the morphological traits of the progeny. In this study, the total dry mass of seedlings showed a stronger relationship with the root dry mass than the leaf and stem dry masses (Table 6), indicating the major contribution of the root system to plant dry mass. In general, among all traits, the seedling height was most significantly affected by all factors and their interactions. The results reveal that taller seedlings are produced from seeds that mature on parent plants that are grown under increased temperatures, treated with higher GA$_3$ levels, and germinated under higher temperature regimes.

5. Conclusions

This study has clearly shown that applying GA$_3$ during seedling growth promotes flowering in all populations of evening primrose, which flowered in the first year rather than in the second year. However, seeds that matured on the parent plants of these populations varied in germinability. Additionally, the seeds that matured under higher temperatures were more germinable and germinated faster than the seeds that matured under lower temperatures. Higher temperatures during seedling growth also led to taller seedlings, but lowered total dry mass. Parent plants that were treated with higher GA$_3$ levels resulted in taller seedlings with more leaves. From these findings, it can be concluded that differences
among populations of evening primrose may have a genetic basis. Moreover, maturation temperature influences seed traits, and differences in seed performance can be seen during seed incubation and seedling growth. Further studies in other biennial plants may shine more light on the effects of such factors on parent plants and their progenies.

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