



Phenotypic plasticity as the main driver of alien plant trait variation in urban versus rural microclimate for the model species *Veronica persica*

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Abstract

Urban environments are warmer than the rural surroundings, impacting plant phenotypic traits. When plants are present over areas with contrasted conditions such as along urbanization gradients, their phenotypes may differ, and these differences depend on different processes, including phenotypic plasticity, maternal environmental effects and genetic differentiation (local adaptation and/or genetic drift). Successful establishment of alien species along environmental gradients has been linked to high phenotypic plasticity and rapid evolutionary responses, which are easier to track for species with a known residence time. The mechanisms explaining trait variation in plants in urban versus rural microclimatic conditions have received little attention. Using the alien *Veronica persica* as model species, we measured leaf traits in urban and rural populations and performed a reciprocal common-garden experiment to study how germination, leaf, growth, and flowering traits varied in response to experimental microclimate (rural or urban) and population origin environment (rural or urban). *Veronica persica* displayed phenotypic plasticity in all measured traits, with reduced germination, development, and flowering under urban microclimate which suggests more stressful growing conditions in the urban than in the rural microclimate. No significant effect of the rural or urban origin environment was detected, providing no evidence for local adaptation to urban or rural environments. Additionally, we found limited signs of maternal environmental effects. We noted the importance of the mother plant and the population identities suggesting genetically based differences. Our results indicate that urban environments are more hostile than rural ones, and that *V. persica* does not show any adaptation to urban environments despite genetic differences between populations.

Keywords Urbanization · Urban microclimate · Trait variation · Plasticity · Adaptation

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Introduction

Cities are known for their warmer microclimate compared to the countryside, a phenomenon referred to as the *urban heat islands effect* (UHI, Oke 1981a, b). The percentage of impervious surfaces, like concrete or asphalt, is positively linked to the intensity of these UHI effects (Oke 1981a, b; Ward et al. 2016). While UHI effects are the most visible at the kilometer scale, a diversity of cooler and warmer microhabitats occurs at the scale of tens of meters to a few meters due to the high heterogeneity of the urban environment (Ren et al. 2013). This high diversity in local conditions results from the complexity of the urban matrix, composed of anthropogenic structures of varying height and spacing, which affects the local energy fluxes and leads to microscale temperature variations (Grimmond et al. 2001). Because of this urban matrix, areas available for plant growth are also limited and subject to varying disturbances (Gorton Amanda et al. 2020). Habitat fragmentation due to urbanization can isolate plant populations (Ortega and Pearson 2005). Because of its effects on environmental conditions, urbanization can thus represent particular growing areas for plants and could lead to phenotypic variation, possibly due to the selection of adaptive traits (Alberti et al. 2003; Franks et al. 2007).

Phenotypic plasticity, the capacity of a genotype to generate various phenotypes in different environments, allows plants to respond to abiotic conditions (David et al. 2013; Nicotra et al. 2010). Therefore, high phenotypic plasticity may be an important strategy for species growing along an urban-to-rural gradient, as it enables individuals to accommodate to highly heterogeneous conditions (Borowy and Swan 2020). On the other hand, key variables for individual fitness such as plant life-history traits (e.g., germination success and timing, flower and seed number, etc.) can be under strong selection pressure from environmental conditions (Gorton et al. 2020; Rivkin et al. 2019). Urban conditions may therefore impose selection on the population gene pool, which can lead to local adaptation—visible by a higher fitness of local populations in the local environment than in foreign environments (Donihue and Lambert 2015). Local adaptation is also associated with restricted gene flow among populations (Lortie and Hierro 2021). However, the genetic structure of plant populations is not just the result of selection, but can also be impacted by genetic drift—the random fluctuation of allele frequencies, particularly important in small and isolated populations (Hagenblad et al. 2015). Finally, the phenotype of an individual is not only due to its genotype and the environmental conditions it experiences, but possibly also to maternal environmental effects—influences of the maternal phenotype on the phenotype of its offspring,

via mechanisms exclusive of any genetic information (Donohue 2009; Galloway and Etterson 2007; Gutterman 2009; Latzel 2015; Latzel et al. 2021; Marshall and Uller 2007; Mousseau and Fox 1998; Roach and Wulff 1987). For plants, maternal environmental effects are typically mediated by seed provisioning (Baskin and Baskin 1998). Within the same species, heavier and larger seeds often positively influence germination probability and speed, and thus the development of the seedlings (Baskin and Baskin 1998).

Even if plant phenotypic trait variation has been studied in relation to urbanization (Borowy and Swan 2020; Géron et al. 2021), the exploration of the mechanisms associated with such trait variations is still in its infancy (but see Géron et al., 2022). A few studies have detected rapid local adaptation of native plant species to urban conditions. For example, Cheptou et al. (2008) found that urban populations of *Crepis sancta* exhibited higher fitness when grown in urban areas compared to rural areas. This difference was attributed to reduced dispersal abilities in urban populations caused by a high dispersal cost in cities. Gorton et al. (2018) highlighted adaptive genetic differentiation in flowering time in urban populations of *Ambrosia artemisiifolia*, and Thompson et al. (2016) suggested that selection was acting against cyanogenesis in urban populations of *Trifolium repens*. Yet, studies disentangling the roles of phenotypic plasticity, local adaptation, and maternal environmental effects as sources of trait variation between urban and rural populations of plant species are rare. Gaining a detailed understanding of how urbanization influences plant species and the underlying processes is crucial. This is especially significant due to the accelerated and intensified climate change effects experienced in urban areas compared to rural regions (Bader et al. 2018; Brans et al. 2017). Alien plant species represent opportunities to better understand ecological and evolutionary processes (Monty and Mahy 2009; Parker et al. 2003). Some are very common and can be found in many environments, for example along the urbanization gradient (Štajerová et al. 2017). Moreover, as the date of first observation in the introduced range is often known (Hagenblad et al. 2015), so is the period available for possible evolutionary response to novel environmental conditions. Some studies have stressed that high phenotypic plasticity is crucial to successful colonization of alien plants (Parker et al. 2003), while others have shown that rapid evolutionary processes are most important (Buswell et al. 2011; Dlugosch and Parker 2008).

In this study, we attempted to identify the sources of variation of several traits (related to germination, leaf ecophysiology, growth, and flowering) of the model alien plant species *Veronica persica* Poir. (Plantaginaceae) in response to rural vs urban microclimate. We analyzed field-measured traits and performed a reciprocal common-garden experiment with populations from rural and urban areas.

We assessed the importance of maternal environmental effects, phenotypic plasticity, and genetic differentiation on the measured traits. We hypothesized that (i) plants would display phenotypic plasticity in relation to the microclimatic conditions, with a more constrained development in urban microclimate; (ii) plants from urban origin environments would display a higher fitness in urban microclimate and plants from rural origin environments would have a higher fitness in rural microclimate, which would be the sign of a local adaptation to their origin environment; (iii) seed mass would influence the trait variation in *V. persica*, indicating maternal environmental effects.

Methods

Model species

Veronica persica is an annual herbaceous plant of the Plantaginaceae family, native to the north Caucasus and Iran (Kew Gardens 2021). It has a creeping growth, with stems reaching up to 60 cm. *V. persica* has sessile flowers, is entomogamous and can be self-pollinated, and does not seem to have a single mode of seed dispersal (e.g., mainly autochory, but seeds can also be dispersed by water or animals; Infloweb 2021; Kleyer et al 2008; Masaryk University 2021; Wild et al., 2019a). It germinates in autumn or early spring and flowers during the following late spring–early summer (Bond and Turner 2007). This species is now present worldwide and considered as a crop weed (Kew Gardens 2021). *V. persica* was introduced in Belgium during the beginning of the nineteenth century and is now widespread in the country (Verloove 2021). It was chosen as a model species because of its abundance in Belgium both in urban and rural areas, and for its small size and fast life cycle, facilitating its use in an experimental set-up.

Field populations and seed harvest

We chose the Atlantic biogeographical region of Belgium [European Environment Agency (EEA) 2011], i.e., the area north of the Meuse river, as the study area. This spatial delineation was chosen to keep the background climatic conditions as homogeneous as possible. The study area has a temperate oceanic climate, with relatively cool and wet summers, and mild and humid winters [Royal Meteorological Institute (RMI) 2021]. It encompasses Flanders, Brussels Capital Region, and the north of Wallonia, containing some of the most urbanized parts of Belgium (De Ridder et al. 2015).

We selected 18 populations of *V. persica*; nine from rural origin environments and nine from urban origin environments (Fig. 1, Supplementary information: Table S1).

Urbanity was assessed using remotely sensed urbanity (EEA 2019), here defined as the percentage of sealed surfaces at 400 m² resolution. This urbanity scale allowed us to take into account the differences in microclimatic conditions due to urbanization (Brans et al. 2017; Kaiser et al. 2016). Following Brans et al. (2017) and Kaiser et al. (2016), we have considered as coming from urban origin environment the populations whose urbanity is higher than 16%. Each of the 18 populations was at least 4 km apart, and each population consisted of ca. 30–50 *V. persica* individuals (Fig. 1). ArcMap 10.5.1 (ArcGis Desktop, 2017) was used for spatial processing.

In mid-May 2019, we collected 40 seeds from 10 randomly chosen individuals (called mother plants hereafter) from each of the 18 populations. We excluded individuals with obvious damages or that had been cut or mown. We visually sorted the seeds under binoculars to remove damaged ones. We then weighed to the nearest 0.1 mg (Dual-Range XA105, Mettler Toledo, Columbus) four lots of five randomly chosen seeds. Seed lots were considered because of the very small mass of individual seeds. The mass of each five-seed lots was divided by 5 to obtain individual seed mass estimates. We conducted a germination test on the remaining seeds: we placed five seeds per mother plant of each population in Petri dishes, on moistened filter papers with distilled water, which we put in an incubator (POL-EKO Aparatura, Wodzisław Śląski) with 12 h of light at 25°C. After 2 weeks, the germination rate across all populations equaled 83%.

The Specific Leaf Area (SLA) relates to the individual resource uptake strategy, with lower values in typically harsher growing conditions (Gregg et al. 2003; Song et al. 2019). We measured the SLA at the population locations in the field (in situ) to test if urban and rural populations differed in this leaf trait. In May 2021, the three latest developed leaves were collected on ten individuals per population in situ. We scanned the fresh leaf area using a flatbed scanner, and we used the scans to measure leaf area in ImageJ (Rasband 2018). We weighed the dry leaf mass after drying them at 60 °C for 48 h. We calculated the SLA following $SLA = \frac{\text{leaf area (cm}^2\text{)}}{\text{dry mass (g)}}$ and averaged per plant.

Reciprocal common-garden design and follow up

To investigate the sources of trait variations in relation to microclimate and population origin environment (phenotypic plasticity, local adaptation, and maternal environmental effects), we conducted a reciprocal common-garden experiment under urban and rural microclimates, located at the Biodiversity and Landscape laboratory of Gembloux Agro-Bio Tech, University of Liège (50°33'49.2"N, 4°42'09.2"E).

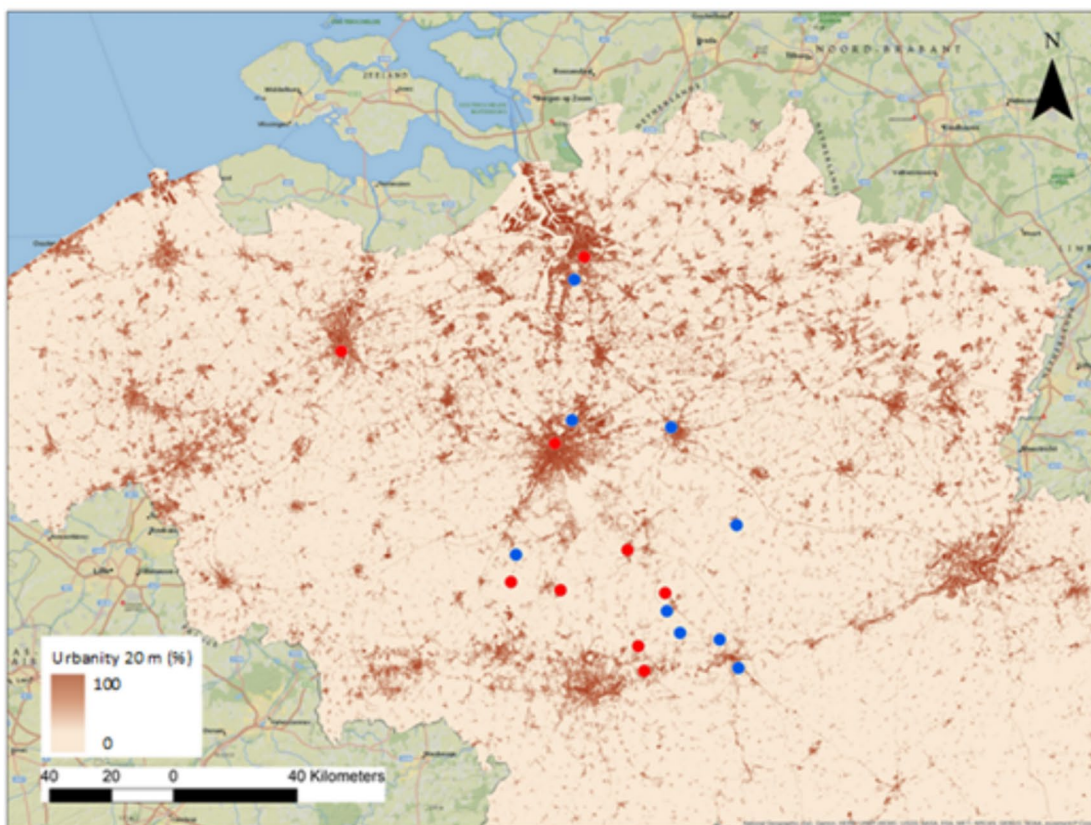


Fig. 1 Locations of the populations of *V. persica* in Belgium, urban populations are represented by red circles, and rural populations are represented by blue circles. Top: topographical map; bottom: urbanity at 20 m². Note that the dot size is bigger than the resolution of the maps for readability

The urban microclimate garden (hereafter called the urban microclimate treatment) was located in a parking lot with asphalt and no trees, close to buildings and with high solar exposure toward the east, south and west. The rural microclimate garden (hereafter called the rural microclimate treatment) was located along the edge of a mown grassland, with no anthropogenic structures, a full vegetation coverage of the soil, and a good exposure to the sun in all directions. The two gardens were ca. 200 m apart.

For each garden, the experimental design consisted of two metal grids of 2.5 × 2 m (grid cell dimensions: 10.5 × 10.5 cm), in which pierced plastic pots of 10 × 10 cm with a capacity of 0.75 L were inserted. The metal grids were elevated 15 cm above the ground with concrete blocks, to make sure that the pots did not touch the asphalt or vegetated ground, which would block their drainage. The vegetation at and around the rural garden was mown before installation.

In each garden, we randomly placed a total of 360 pots (10 mother plants × 18 populations × 2 replicates). We filled each pot with nutrient rich clay-loam soil considered as an ideal substrate for *V. persica* (Infloweb 2021). Because *V. persica* is a creeping plant, we recorded the temperature just below the soil surface (ca. 0 cm) with TMS 4 sensors (every 15 min, TOMST, Prague, Wild et al. 2019b). Four TMS 4 sensors were placed in each garden; each one placed in a separate pot that was filled with soil but not sown with seeds. Additionally, two rain gauges were placed in each garden, each in a pot that was not sown, to record precipitation quantities.

On March 17th, 2021, we saturated the soil of the pots of the rural and urban microclimate gardens with water, and we did sow all the pots on the next day. The prepared five-seed lots were placed on top of the soil of an individual pot and then covered with a 0.5 cm soil layer. As such, we sowed 20 seeds per mother plant from each plant population in total (two lots of five seeds, in two different pots, in the urban microclimate, and two lots of five seeds, in two different pots, in the rural microclimate). We randomly placed the pots in each garden and we randomly changed their positions every 2 weeks. The plants were not watered other than by rain for the duration of the experiment.

We counted the germinations every 2 days from the sowing day until no more germination was seen during a period of 14 days. We defined the *germination percentage* as the proportion of seeds that germinated out of the five-seed lots. We kept the first germinated seedling and removed all others to rule out intraspecific competition. We waited 1 week after

the first seeds had germinated to make sure that the seedling was viable, and then removed all subsequent germinations in the same pot, so only the earliest germinated seed per pot remained. For each pot, the first seed that germinated was used to determine the *germination delay*, i.e., number of days between the sowing and the first germination.

We counted the cumulative number of flowers (spent flowers, open flowers, and formed buds) every 2 days, from the day the first flower appeared in the rural or urban garden until the end of the experiment (17th week). At the end of the experiment (17th week), we determined the final number of spent flowers, open flowers and formed buds, hereafter referred to as the *flower number*. We calculated the *flowering delay* (in days) for each plant as the difference between the germination day and the day on which the first flower was counted.

At the end of the flowering period, in early July, we harvested the three latest fully developed leaves of each plant, measured the fresh leaf area and the leaf dry mass, calculated the *SLA* as above, and averaged it per individual. At the end of the experiment (in the 17th week), we collected the aboveground biomass of each plant, dried it at 60 °C for 48 h, and then weighed it to the nearest 0.1 mg (DualRange XA105, Mettler Toledo, Columbus). We added the weight of the three leaves harvested for the *SLA* to obtain the *above-ground dry biomass*.

Statistical analyses

Microclimate variables

We compared the surface temperature and the precipitation measured at the urban and rural microclimate treatments at the reciprocal common-garden. The average surface temperature was 1.21 °C higher in the urban microclimate (mean ± SE: 13.21 °C ± 0.10, 12.00 °C ± 0.10 for the urban and rural microclimate treatment, respectively; Supplementary information: Figure S1), while the total precipitation equaled 1.76 and 1.63 L per pot (100 cm², 176 and 163 mm measured during the experiment in the urban and rural microclimate, respectively).

Seed mass

To understand if populations from urban and rural origin environments differed in their seed mass variance, we tested the equality of variances in seed mass between rural and urban populations with a Levene's test. As the variances were different, a rank transformation was performed before testing for differences in average seed mass using a nested ANOVA with origin environment (rural vs urban) as fixed factor and population as random factor nested in origin environment.

SLA measured in situ

The relationship between the SLA variable measured in situ and the origin environment (rural vs urban) was analyzed using a linear mixed model (R package lme4 Bates et al., 2020). We included population identity as a random factor nested in origin environment, and mother plant identity as a random factor nested in population, to take into account our hierarchical sampling design.

Reciprocal common-garden experiment:

The traits measured in the reciprocal common-garden were analyzed using an ANCOVA with origin environment (rural vs urban) as fixed factor, microclimate treatment (rural vs urban microclimate) as fixed factor, population as random factor nested in origin environment, mother plant identity as random factor nested in population, and seed mass as covariate. We included the interaction between the origin environment and microclimate treatments in the models.

Each factor, covariate or interaction in the model represents a potential source of phenotypic trait variation. The microclimate factor reflects phenotypic plasticity induced by microclimatic differences between the rural and urban gardens, at the family (i.e., same mother plant) level. A more direct test for plasticity would use clones, but as *V. persica* is not a clonal plant, we used half-sibs to quantify the plastic response between gardens. The origin environment factor reflects genetically based differentiation between rural and urban population groups. A significant microclimate \times origin environment interaction would reflect genetic differentiation among origin environments on the level of phenotypic plasticity in response to microclimate. Local adaptation would be detected if a significant effect of the origin environment factor would be found which would mean that populations from rural origin environments would outperform populations from urban origin environment under rural conditions, and/or that populations from urban origin environments would outperform populations from rural origin environment under urban conditions. If this is not observed, differences between origin environments could be interpreted as the result of genetic drift or adaptation to factors not studied here. The random factor population corresponds to genetic differentiation within urban or within rural areas. The seed mass covariate reflects maternal environmental effects on phenotypic trait variation. The random factor mother plant corresponds to the influence of mother plants identity on their offspring beyond the factors already considered above, whether through genetic differences between populations or maternal environmental effects.

The germination percentage was transformed using $Y = \arcsin(X - 1)$ and the flower number was log-transformed to improve homoscedasticity. As no other

transformation could improve homoscedasticity, the above-ground dry biomass was rank-transformed. Analyses were performed with Minitab ver. 21.1 (“Minitab Statistical Software”, 2021) and R, version 3.5.2 (R Core Team 2023).

Results

Seed mass and SLA variation at the population location

Seed mass was not significantly different on average between the urban and rural origin environments ($Df = 1$; $F = 0.5$; $P = 0.491$), but the seed mass variance was higher for the urban origin environment (Levene’s test, $F = 2.33$, $P = 0.002$, Fig. 1). The SLA was not significantly different between origin environments in the field ($Df = 1$; $F = 0.56$; P value = 0.464, not plotted).

Traits variation in the reciprocal common-garden experiment

As shown in Table 1, all the measured traits were significantly different between the rural and urban microclimates. In the urban microclimate, seeds germinated later and with lower success, and the plants produced a lower number of flowers, flowered later, had lower SLA values and lower biomass (Fig. 2, Table 2).

The factor origin environment was not significant, nor was its interaction with microclimate (Fig. 2, Table 1).

A population effect and a mother plant effect were found for all traits except SLA for both and biomass for the latter (Table 1). The covariate seed mass had a significant influence only on the biomass (Table 1).

Discussion

Despite the absence of clear patterns in traits measured in situ in urban and rural populations, *V. persica* exhibited significant differences in all measured traits between the urban and rural microclimate treatments of the common-garden, highlighting robust phenotypic plasticity. Conversely, we observed no significant effects of origin environment and minimal impact of seed mass on the measured traits, suggesting a lack of local adaptation of populations from urban origin environments to urban microclimate or of populations from rural origin environments to rural microclimate, and a limited influence of maternal environmental effects. Nevertheless, we observed variations in most traits among populations and mother plants.

The plants growing in the urban microclimate treatment had a lower fitness, whatever their origin environment,

Table 1 Results of the ANCOVA performed on the traits measured in the reciprocal common-garden

Source of variation	Germination percentage			Germination delay			Flower number			Flowering delay			SLA			Aboveground dry biomass		
	Df	F	P value	Df	F	P value	Df	F	P value	Df	F	P value	Df	F	P value	Df	F	P value
Explanatory variables																		
Seed mass	1	1.57	0.210	1	2.08	0.150	1	0.08	0.800	1	0.15	1	1	0.11	0.744	1	5.94	0.020*
Origin environment	1	<0.001	0.960	1	0.32	0.578	1	0.84	0.400	1	0.04	1	1	0	0.960	1	0.16	0.698
Microclimate	1	37.21	<0.001***	1	15.50	<0.001***	1	572.6	<0.001***	1	34.56	<0.001***	1	7.52	0.007**	1	254.14	<0.001***
Origin environment* microclimate	1	0.06	0.806	1	0.25	0.615	1	2.13	0.100	1	0.51	0	1	0.09	0.762	1	0.07	0.787
Random factors																		
Population (origin environment)	16	4.04	<0.001***	16	4.85	<0.001***	16	2.78	<0.001***	16	2.22	0.006**	16	0.40	0.985	16	2.23	0.010**
Mother plant (population)	162	2.45	<0.002**	157	1.72	<0.002**	155	1.60	<0.001***	138	1.43	0.140	133	0.79	0.917	140	1.15	0.176
Error	537			351			348			166			137			217		

Significant effects are in bold and coded as follows: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Germination delay and flowering delay are in days. Germination percentage is in percentage. SLA is in cm^2/g . Aboveground dry biomass is in grams

as evidenced by the lower germination percentage, lower biomass, and lower flower number. Urban microclimate treatment also delayed germination and flowering, and led to lower SLA. Interestingly, phenotypic plasticity was the only source of variation in SLA in our experiment. These results suggest harsher growing conditions in the urban microclimate compared to the rural microclimate for *V. persica* which is in line with our first hypothesis. While no significant differences were observed in situ for the SLA, remarkably similar average SLA values were noted between the rural populations' locations and the corresponding rural microclimate treatment (mean \pm SE: $475.8 \text{ cm}^2/\text{g} \pm 20.5$; and $478.7 \text{ cm}^2/\text{g} \pm 15.2$, respectively). Similarly, comparable SLA values were observed in situ at urban populations' locations and under the urban microclimate treatment (mean \pm SE: $415.4 \text{ cm}^2/\text{g} \pm 22.8$; and $409.8 \text{ cm}^2/\text{g} \pm 12.5$, respectively). This indicates comparable levels of growing condition severity both in situ and under the microclimate treatments in the common-garden experiment. In our case, the precipitation was similar in the rural and urban microclimate treatments, but the latter was 1.2°C warmer on average, so it is likely that the plants in the urban microclimate treatment were exposed not only to warmer growing conditions but also to drier soils due to higher soil evaporation and plant transpiration. In addition, the higher air temperature in the urban microclimate treatment may have lowered the relative humidity of the air, due to the low evapotranspiration associated with the more impermeable environment. The observed level of temperature difference between our urban and adjacent rural environment is in line with the other observations (e.g., 2.5°C warmer daily mean maximum temperature in the city center of Ghent, Belgium relative to the surrounding countryside (Arnds et al. 2017; Caluwaerts et al. 2020; Zhou et al. 2016)). In our case, all the plastic responses observed suggest harsher growing conditions under urban microclimate which have already been observed for other plant species (Ortega and Pearson 2005). In plants, phenotypic plasticity in response to climatic variations is common for many traits, but the direction of the reaction norms may depend on the considered species and climatic conditions (Gorton et al. 2018; Monty et al. 2009; Yakub and Tiffin 2017). For instance, both faster and delayed flowering have been associated with urban conditions, and both faster and delayed germination have been related to warmer or dryer conditions (Franks et al. 2007; Gorton et al. 2018; Neil et al. 2014; Shavruk et al. 2017; Yakub and Tiffin 2017). In contrast, SLA is known to be a highly plastic trait and lower SLA values are typically linked to less optimal conditions, such as warmer and drier climates (Lamarque et al. 2015; Monty et al. 2013; Sun et al. 2020). Furthermore, urban microclimate and higher temperatures have been associated with a lower germination percentage,

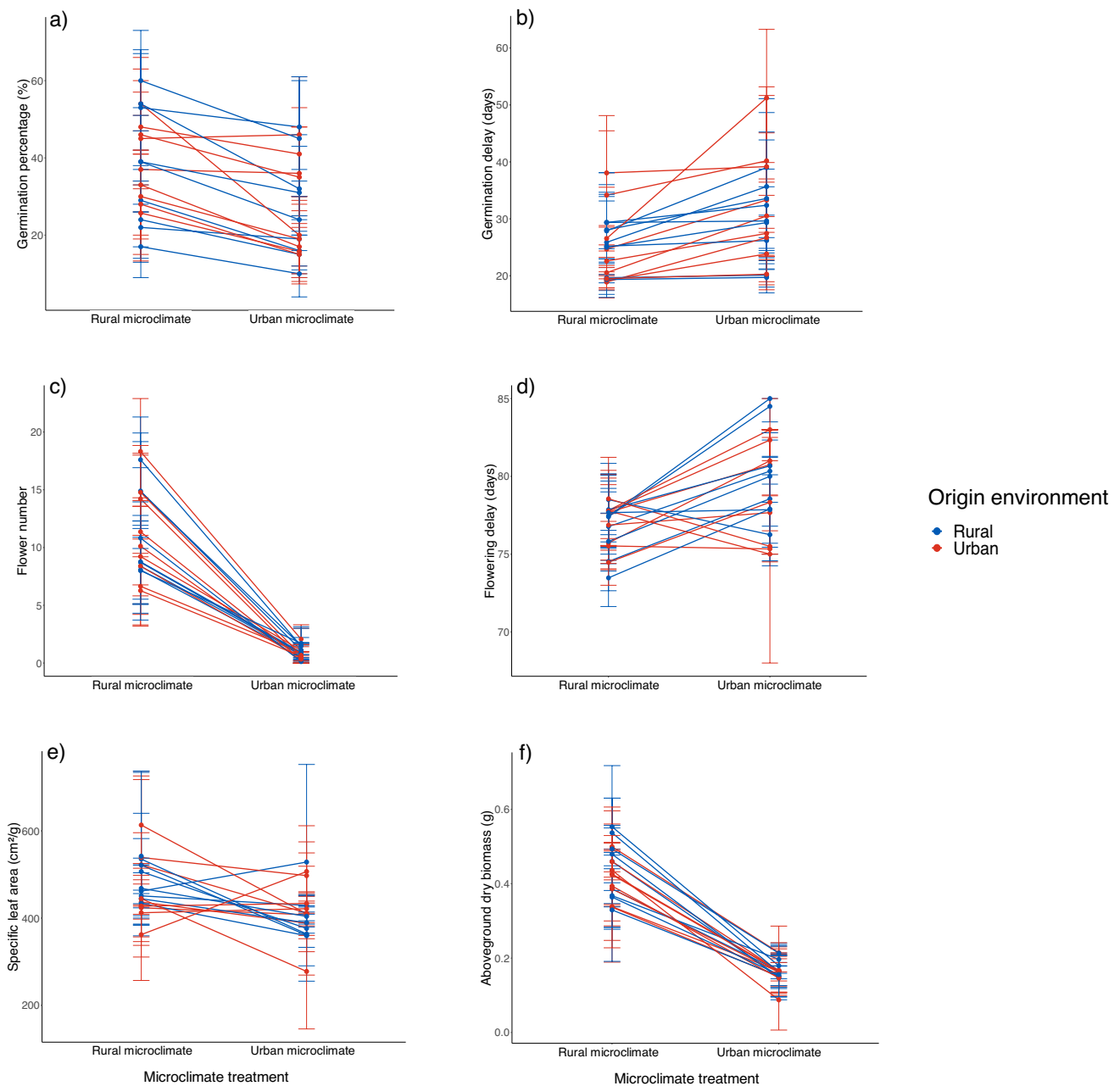


Fig. 2 Reaction norms to the microclimate treatment, for the germination percentage, germination delay, flower number, flowering delay, specific leaf area (SLA), and aboveground biomass of *V. persica*. The

18 populations are colored by their origin environment, blue for rural populations, and red for urban populations. 95% confidence intervals are represented for each of the populations by the error bars

in accordance with our findings (Finch-Savage and Leubner-Metzger 2006; Gremer et al. 2016; Piana et al. 2019).

Contrary to our second hypothesis, we did not detect any genetically based trait differences between rural and urban origin environments. Therefore, no signs of local adaptation of urban populations to urban microclimate, or of rural populations to rural microclimate, were found. This contrasts with the, albeit few, studies that found local adaptations of native plants to urban environments

(flowering time: Gorton et al. 2018; leaf pigment: Thompson et al. 2016; height and number of leaves: Yakub and Tiffin, 2017). On the other hand, Pisman et al. (2020) studied how life-history traits of *Taraxacum officinale* varied in function of herbivory and urban-to-rural gradients in Belgium and did not find any differences in the dry weight or flower number between plants from urban and rural origin environments in a common-garden experiment. The absence of local adaptation in *V. persica* populations might

Table 2 Mean and standard deviation (sd) for each of the six traits measured in the reciprocal common-garden, within the microclimate (rural or urban) and origin environment (rural or urban) conditions

Treatment	Germination percentage		Germination delay		Flower number		Flowering delay		SLA		Aboveground dry biomass	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Microclimate												
Rural	0.38	0.31	24.67	13.17	11.35	9.36	76.48	4.4	478.7	217.77	0.44	0.22
Urban	0.27	0.28	29.71	17.27	0.93	1.7	79.27	4.19	409.76	118.55	0.17	0.09
Origin environment												
Rural	0.32	0.3	26.68	14.87	6.55	8.52	77.19	4.55	465.08	190.35	0.36	0.24
Urban	0.33	0.3	27.25	15.87	6.56	8.88	77.21	4.48	451.51	200.08	0.33	0.21

Germination delay and flowering delay response variables are in days. The germination percentage response variable is in percentage. SLA is in cm^2/g . Aboveground dry biomass is in grams

be due to important gene flow (Slarkin 1985), which is dependent on pollination and seeds dispersal. Despite the fragmented urban habitat, the populations of *V. persica* might still be genetically connected, because this species is pollinated by insects and urban areas often host a significant abundance of pollinator species (Hall et al. 2016). Additionally, *V. persica* has many dispersal modes, and transport of seeds via animals, water, or traffic might facilitate genetic mixing and counteract genetic differentiation (Kawecki and Ebert 2004). It has to be noted, however, that the random effect of population was significant for most of the studied traits in the experiment, indicating a genetically based variation among the sampled populations, regardless of their urban or rural origin environment. Such a pattern can be related to genetic drift and/or colonization history (Keller et al. 2009; Monty et al. 2009), but the present study cannot rule out that adaptation still occurred in response to other selection pressures than urbanization and its effects on environmental conditions. To better detect local adaptation, the first generation of individuals could be grown under common conditions rather than the individuals derived from seeds collected in the populations' environment of origin (Latzel 2015; Monty et al. 2009; Rossiter 1996), though this can artificially hide the role of maternal environmental effects. Other factors that may have affected our capacity to detect local adaptation are the scale at which urbanization was considered which was probably too coarse to capture the microclimatic effects of urbanization as very local variations of environmental conditions (at the scale of the individuals) have been detected to highly influence alien plant development for example (Géron et al. 2021). Finally, despite the annual life cycle characteristic of our model species, the observed absence of adaptive differentiation could also be attributed to the species' relatively brief residence time in the region, with the number of generations

proving insufficient for discernible adaptive processes to unfold (Verloove 2021).

We found that maternal provisioning (through the effect of seed mass) was not an important source of trait variation for *V. persica* in our experiment, which went against our third hypothesis. A possible reason for the lack of effect of seed mass might be the fact that we weighed the seeds in batches, because their individual weights were too low, and consequently did not monitor each seed sown independently. As such, even if we did not detect maternal environmental effects in our study, it is still possible that they were present. Maternal environmental effects have received comparatively less attention than local adaptation in the study of the sources of plant trait variation in general and in the context of urbanization in particular (Donohue 2009; Donohue and Schmitt 1998). However, previous work has found strong maternal environmental effects especially when mother plants faced uncertain offspring environments. The latter can be the case for city areas where environmental conditions are heterogeneous in space and time (Baskin and Baskin 1998; Donohue 2009; Galloway and Etterson 2007; Géron et al. 2022; Gianella et al. 2021; Grimmond 2007; Latzel et al. 2021; Nicotra et al. 2010).

Experimental reciprocal common-garden studies allow for disentangling the different processes responsible for trait variation, by manipulating some sources of variation and controlling for others. Yet, since our experiment was performed outdoors, the specific climatic conditions during the experimental period, though representative of the region, may have influenced our results. Moreover, a general single urban or rural microclimate does not exist. To address this, future research could enhance its scope by incorporating a diverse range of microclimates, capturing the different conditions along the urban–rural gradient (Chen et al. 2012; Grimmond et al. 2001).

In conclusion, we found strong evidence for phenotypic plasticity in response to rural versus urban microclimate treatments, with reduced plant performances under urban conditions, but no signs of local adaption and low support for maternal environmental effects. Alien plant species have been present for a relatively short period of time, and often in great numbers along the rural-to-urban gradient (McKinney 2006), and therefore represent suitable study models for understanding plant response to urbanization (Géron et al. 2022; Gorton et al. 2020; Rivkin et al. 2019). Even if processes revealed for a specific model species might not apply for other study species, improving our knowledge of the impacts of urban environments on organisms is very valuable. Adaptations in plants, and the absence thereof, may become an increasingly important topic as cities experience the effects of global change more rapidly and more strongly than rural areas (Bader et al. 2018; Brans et al. 2017).

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Availability of data and code The data presented in this study are openly available on Figshare with the following. <https://doi.org/10.6084/m9.figshare.26346703.v1>.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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