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1 **ARTICLE**

2

3 Temporal fitness fluctuations in experimental *Arabidopsis thaliana* populations

4

5 **Keywords:** fitness fluctuations, genetics of adaptation, *Arabidopsis thaliana*

6

7

8 Abstract

9 Understanding the genetics of lifetime fitness is crucial to understand a species'
10 ecological preferences and ultimately predict its ability to cope with novel
11 environmental conditions. Yet, there is a dearth of information regarding the impact of
12 the ecological variance experienced by natural populations on expressed phenotypic
13 and fitness differences. Here, we follow the natural dynamics of experimental *A. thaliana*
14 populations over 5 successive plantings whose timing was determined by the natural
15 progression of the plant's life cycle and disentangle the environmental and genetic
16 factors that drive plant ecological performance at a given locality. We show that, at the
17 intermediate latitude where the experiment was conducted, a given genotype can
18 experience different life cycles across successive seasons. Lifetime fitness across these
19 seasons varied strongly, with a fall planting yielding 36-fold higher fitness compared to
20 a spring planting. In addition, the actual life-stage at which plant overwinter oscillated
21 across years, depending on the timing of the end of the summer season. We observed a
22 rare but severe fitness differential after inadequate early flowering in one of the five
23 planting. Substrate variation played a comparatively minor role, but also contributed to
24 modulate the magnitude of fitness differentials between genotypes. Finally, reciprocal
25 introgressions on chromosome 4 demonstrated that the fitness effect of a specific
26 chromosomal region is strongly contingent on micro-geographic and seasonal

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1 fluctuations. Our study contributes to emphasize the extent to which the fitness impact
2 of phenotypic traits and the genes that encode them in the genome can fluctuate.
3 Experiments aiming at dissecting the molecular basis of local adaptation must
4 apprehend the complexity introduced by temporal fluctuations because they massively
5 affect the expression of phenotype and fitness differences.
6

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1

2 **Introduction**

3 There is overwhelming evidence that local selection pressures have continuously
4 shaped the genetic composition and ecological performance of natural populations [1-3].
5 But in the context of rapid climate change, greater attention must be devoted to the
6 processes by which species can evolve to adjust their ecological niche [4-6]. The
7 phenotypes that plants deploy in nature, i.e. their timing of germination, their growth
8 rate, their timing of reproduction, are plastically regulated by environmental conditions
9 that vary both temporally and geographically [7]. Much is known about the molecular
10 mechanisms of many plastic plant traits [8-10]. By contrast, we know little about how
11 environmental fluctuations influence the amount of phenotypic variation that is actually
12 expressed in natural conditions, nor do we know how it impacts population levels of
13 fitness variance, an elemental requirement for adaptive evolution [11]. Here we
14 document seasonal variation in expressed plant life cycles and measurements of fitness
15 in *Arabidopsis thaliana*, a plant species that stands as a model for the dissection of
16 molecular modifications underpinning local adaptation [12]. In this species, analyses of
17 genetic variation along altitudinal transects often revealed patterns of local adaptation
18 [13-15]. Patterns of nucleotide variation uncovered the population genetics signatures
19 of local adaptation on a diverse panel of traits [16-20]. Reciprocal transplants of a
20 Swedish and an Italian population suggested phenotypic trade-offs evolved in
21 Scandinavian populations [21,22] and common garden experiments in four different
22 climatic zones highlighted the hundreds of nucleotide variants that associate with local
23 measures of fitness [23]. While these studies reveal the pervasive impact of local
24 selective forces across the range of the species, little is known about the actual
25 ecological challenges populations are exposed to locally and that may lead to this

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1 pattern[24]. Because both the environmental conditions and the genetics of specific
2 individuals can vary, the prediction of which plastic traits will be displayed by any one
3 individual and whether it will impact fitness is far from straightforward [25,26]. It is
4 generally understood that local temporal variance of environmental conditions will
5 impact expressed phenotypes and associating fitness levels. Yet, this phenomenon was
6 seldom monitored. At the extremes of the species range, measures of fitness fluctuate
7 across seasons [21,27]. Instead, in climatic regions were summers are sufficiently mild
8 and wet to allow the completion of multiple generation each year, it is unclear how
9 patterns of fluctuations will be affected. Does seasonal variance have cascading effects
10 on expressed life cycles? Does it impact the magnitude of phenotypic and fitness
11 differences manifested by diverse genotypes? Does life history plasticity tend to buffer
12 differences? How does the effect of temporal variance compare with the magnitude of
13 microgeographic or genetic variance?
14 To answer these questions, we designed an experiment that dissects how environmental
15 factors carve fitness profiles in natural populations at intermediate latitude. We report
16 the monitoring of lifetime fitness in experimental populations over 5 natural successions
17 of plant cycles in conditions differing in soil substrate and water availability. We
18 monitored 4 genotypes, including two genomic backgrounds, one of local and one of
19 distant origin (Col-0 and C24), and the reciprocal chromosome 4 (Chr 4)-introgressions
20 of several polymorphisms previously reported to associate with differential fitness in
21 various locations [23]. Our experiment demonstrates that overall fitness results from
22 complex interactions between seasonal oscillations, soil composition, genomic
23 background and genotypes, leading to marked fluctuations in the phenotypic and fitness
24 differences expressed at a given locality under natural conditions.
25

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1

2 **Material and methods**

3 **Genetic plant material**

4 *Arabidopsis thaliana* is an annual weed growing across a broad geographic range [28].
5 The fruits it produces are called siliques, a character of the Brassicaceae family. In this
6 study, we monitored field performance of two wild type genotypes, Col-0 and C24.
7 Genomic information for these two lines suggest that the Col-0 genotype is typical of
8 Western European populations whereas C24 is more related to Southern European
9 genotypes [29]. We further included in our experiment two reciprocal near-isogenic
10 lines (NILs). The two sets of NILs contained either an introgression of chromosome 4,
11 between 11.8 to 13.8Mb, of C24 accession in Col-0 genomic background or a genomic
12 fragment between 5.1 and 15.3Mb of Col-0 accession in C24 background [30]. Our
13 experiment thus includes genomic background and chromosome-4 introgression as two
14 separate genetic factors. In total, Col-0 and C24 differed for 284 of the 867 SNPs
15 reported to associate with local survival and seed production in *A. thaliana* [23]. Of
16 those, 25 (8%) and 38 (13%) SNPs mapped to the introgressed fragments in Col-0 and
17 C24 backgrounds, respectively. They associated with enhanced survival in Finland and
18 silique number in Spain for the Col-0 genotype [23].

19

20 **Field plantings**

21 In this study, we monitored germination, flowering time and fitness of the 2 wild type
22 genotypes, Col-0 and C24 and their reciprocal Chr4 introgressions in the field over five
23 consecutive generations that followed a quasi-natural population establishment
24 dynamics. The field was located in the middle of a flat grass meadow and fenced with

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1 iron nets to prevent grazing by rabbits. No vegetation protected it from sun or wind. We
2 filled large flat pots (30cmx40cmx12cm) with two soil types: Arabidopsis turf soil
3 (Einheitserde Typ Minitray, plus 1kg Osmocote Start per m^3, Einheitserde Werkverband,
4 Sinntal-Jossa) or a soil mixture enriched in sand (a 1:3 mixture of the turf described
5 above and sand). Pots thus dried faster in the sand mixture compared to turf. Pots were
6 randomized and placed on a large plastic cover that prevented germination from the soil
7 below (Suppl. Fig.1). Each replicate population was prepared in a pot by sowing seeds
8 mixed with 5 g silicon dioxide (Sigma-Aldrich, S5631). Pots had been watered to
9 saturation to facilitate seed adhesion to the soil. After sowing, seeds were left exposed to
10 natural conditions in the field and no watering other than natural rain was done. The
11 first planting was started with seeds fully ripened in the greenhouse. All other plantings
12 were started with seeds collected in the field in the previous planting, with the exception
13 of C24 seeds in planting 4, which were taken from planting 2 (the C24 genotype did not
14 survive winter in planting 3). At complete senescence, plants were collected and dried in
15 paper bags and seeds were harvested. Immediately after harvest, 50 field-collected
16 seeds (taken from a pool of 500 seeds collected from 5 plants per pot) of the two NILs
17 and their wild-type parents were placed in 12 replicate pots, for each of the two soil
18 compositions and 4 genotypes. There were two exceptions to this scheme: planting 1
19 was started with 200 seeds and conducted in only four replicates (32 pots), and planting
20 5 was performed with only Col-0 and Col^{NIL} due to limitation in personnel (48 pots). The
21 timing of the different plantings is given in Fig. 1.

22 For all plantings, seedlings other than *A. thaliana* were immediately removed when they
23 appeared. Our experiment included empty pots to evaluate whether migration occurred
24 between pots. After detecting migrants in control pots, we verified the genotype of each
25 seedling. Individuals with the C24 background display glabrous leaves whereas those of

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1 individuals with the Col-0 background are hairy. The genomic background could thus be
2 verified visually. A leaf was collected from each single plant to extract DNA and genotype
3 the individual at Chr4 by PCR with primers mi05 (5'-CTCTTGCTGCGTAGGGTTCCC-3') and
4 mi06 (5'-ATCTCCCCACTCCCCAATTTT-3'), which generate a length polymorphism at
5 AT4G24415 within the chromosome 4 introgression [31]. We detected 26 heterozygotes
6 in 453 individuals in planting 4, suggesting an outcrossing rate in the field of about 5%.
7 These individuals were removed from further analysis.

8

9 **Fitness and phenotype scoring**

10 For the first planting, early, intermediate and late germinants were observed but the
11 exact germination date was not scored. Germination time was scored for plantings 2-5,
12 flowering time (date of the first open flower) was scored for all five plantings. Silique
13 number was counted for a sample of 3-8 randomly chosen plants in each population. In
14 total, fitness was scored for 96, 401, 583, 301 and 691 plants in plantings 1 to 5,
15 respectively (for a total of 2072 plants). In addition, in plantings 2, 3 and 4, the number
16 of seeds was determined for three siliques in each of 3 randomly chosen plants per
17 population. For fruit number and flowering time, an average was computed for each
18 population (e.g. each pot). The average fruit number per pot was taken as an estimate of
19 lifetime fitness. Variation in average seed number per silique did not change the
20 conclusions based on fruit number (not shown). When plants in a pot failed to germinate
21 or survive until reproduction, lifetime fitness was set to zero. To account for variation in
22 germination rates, we included plant density as a covariate in the analyses (see below).

23

24 **Statistical analysis**

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1 All statistical analyses and figures were performed in R. A generalized linear model
2 (GLM) was used to establish the minimal model explaining phenotypic or fitness
3 variation. For this, we followed the procedure described in Crawley 2005. A first model
4 with average lifetime fruit production as a dependent variable and including, as
5 explanatory variables, the main factors planting, soil type, genomic background and
6 chromosome 4 region, as well as the 2-way, 3-way and 4-way interactions between
7 these factors was run. To take into account variation in fruit number that may result
8 from competition in densely populated pots, the total number of plant in each
9 population was also included as an explanatory covariate. Non-significant interaction
10 terms were removed one by one, from the most complex to the least complex, using the
11 F-test implemented in the R function *drop1.* To control for the non-Gaussian distribution
12 of error, we used a negative binomial distribution of error (implemented in R Package
13 MASS) and tuned its free parameter to adjust the residual deviance to the degrees of
14 freedom of the model. This adjustment was performed at each step of the procedure,
15 until the minimum model was determined. The resulting "minimal" model included the
16 four main factors and the significant interaction terms that remained. Interpreting the
17 effect of a single experimental factor is not straightforward in the presence of
18 interactions between factors, especially when the 4-way interaction is significant. We
19 thus broke down the factors and conducted separate ad-hoc GLM for each genomic
20 backgrounds or for subsets of plantings. The fold-change attributed to experimental
21 factor was calculated by taking the exponential of the log estimates given by the model
22 (GLM with negative binomial distribution of error used the natural log as a link
23 function). This measure corresponds to the odds ratio associated with the factor. The
24 proportion of variance explained by each factor or interaction term, was calculated as
25 the ratio of the deviance computed for a given factor against the total deviance. To

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1 compute the fitness fold-change attributed to the chromosome 4 introgression within
2 each combination of experimental factor (planting, soil composition and genomic
3 background), we ran a separate GLM analysis with introgression as a factor nested
4 within a factor called "setting", which combined soil condition, planting and genomic
5 background in 16 levels. Fitness fold-change attributed to variation in the chromosome
6 4 region was calculated as described above.
7
8
9
10

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1

2 **Results**

3 **Effect of experimental factors on Lifetime fitness**

4 We monitored average fruit (silique) production in experimental *A. thaliana* populations
5 over 5 naturally consecutive plantings by counting the average number of siliques
6 produced per pot (Fig. 1). A generalized linear model with a negative binomial
7 distribution of error adjusted to minimize overdispersion revealed that all factors of the
8 experiment interacted with each other to alter this measure of fitness (Table 1).

9

10 The average number of siliques (fruits) produced in each population was significantly
11 affected by the number of germinants (or survivors) in each replicate population, i.e
12 plant density (*p*= 1.03e-11, Table 1, Spearman coefficient r = -0.30, p= 3.7e-07, Suppl.
13 Fig. 2). This correlation, however, was present only in experimental plots in which
14 germination and survival rates were high, especially plantings 2, 3 and 5 (Suppl. Fig. 2a).
15 Focusing on planting 2, where both backgrounds could be compared, the decrease of
16 silique production associated with increased plant density was only effective for the Col-
17 0 background (Suppl. Fig. 2b). The C24 background, instead, did not yield high density
18 because of a lower germination rate, especially in sand for the planting initiated in the
19 summer (not shown). In the remaining of the analysis, plant density was included as a
20 cofactor, so that the genetic and environmental effect reported below are independent
21 of population density.

22

23 The strongest part of variance was explained by variation across plantings (36% of the
24 variance, p <2.2 e-16, Table 1). Indeed, both highest and lowest values for average
25 silique number per population were observed in planting 3, where most of the

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1 experimental populations with C24 genomic background did not survive (Fig. 2A). As a
2 consequence, the second largest effect was controlled by the interaction between
3 genomic background and planting (18%, p<2.2e-16, Table 1). To characterize the details
4 of average fitness variation across plantings for a single genotype reaching
5 reproduction, we focused on the Col-0 background, which completed its cycle in all 5
6 plantings (Table 2). The log estimate of this analysis revealed that average silique
7 production per plant in planting 3 was 14 times higher than in planting 1, which was
8 itself 2.6 times higher than in planting 5 (Fig. 2B). We thus estimate that, in this
9 experiment, average fruit number per population varied by up to 2.6*14 ~36-fold across
10 plantings for the sole Col-0 genomic background.
11
12 As expected soil quality also had a significant effect on silique production (p =6.07e-06,
13 Table 1), with fitness tending to be lower in sand across all plantings, except in planting
14 3, where growth on sand was advantageous for the Col-0 background (Fig. 3A).
15 Although a relatively small proportion could be attributed to the main effect of genomic
16 background (3%, p= 5.22e-11, Table 1), this factor accounted for a large part of the
17 significant interaction effects with planting and soil. In the three plantings (1, 2 and 4)
18 where the two backgrounds could be compared for fruit production, Col-0 displayed 2-
19 fold greater fitness than C24 in sand, an effect that was not seen in turf (main effect, log
20 estimate 0.85, p= 1.8e-07, interaction with soil, log estimate -0.89, p=9.8e-06, Fig. 3B,
21 Table 3).
22
23 The effect of the chr 4 introgression (Tables 1 and 3) was modulated by all factors,
24 including planting, soil and genomic background (F= 10.42, p=1.67e-13, Table 1). The
25 interaction between planting conditions and background also changed significantly the

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1 effect of the introgression (F=9.7, p<2.2e-16, Tables 1-2). To investigate which factorial
2 combination revealed the effect of the chr4 introgression, we ran a separate GLM
3 analysis with introgression as a factor nested within a factor called "setting", which
4 combined soil condition, planting and genomic background in 16 levels (Fig. 4). This
5 analysis revealed that the effect of the introgression was significant for 3 of the 16
6 settings and its effect was estimated to reverse from a 50% decrease to a 2-fold increase
7 in silique production for the C24 Chr4 allele. Although the introgression of Col-0 into the
8 C24 background was larger than the reciprocal introgression, we detected a significant
9 effect either in both backgrounds or in the Col-0 background only (Fig. 4) suggesting
10 that it is the overlapping portion of the reciprocal introgression that displays fluctuating
11 fitness effects.
12
13 The effect of the introgression, when it is significant, is comparable in magnitude to the
14 2.3- fold increase in silique production per plant of Col-0, compared to the C24 genomic
15 background (Table 3). Thus, in some conditions, the Chr4 introgressed region can reach
16 an effect comparable in magnitude to the average effect caused by the whole genomic
17 background.
18
19 **Effect of experimental factors on life-history variation**
20 We observed that plant lifespan varied drastically across the 5 successive plantings (Fig.
21 1). In the second planting, the life cycle was completed in two months. In planting 3, the
22 life cycle was completed after 8 months and in planting 4, in approximately 4 months.
23 Flowering in planting 4 was terminated in late September (a month later than in
24 planting 2 the previous year), which resulted in a late-fall distribution of seeds for
25 planting 5 and an overwintering at the seed stage.

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1
2 The duration of vegetative growth is believed to have an important impact on final
3 fitness [27,32]. Yet, in our experiment, we observed no obvious correlation between
4 silique production and the duration of the vegetative life cycle (Fig. 5). Col-0 in planting
5 3 yielded slightly higher fitness than planting 2 and 4, despite a much longer period of
6 vegetative growth. Yet, in planting 3, a marginally significant correlation between days
7 to flowering and silique number was observed among the Col-0 individuals that
8 survived the winter (Spearman ρ =0.29, p = 0.07).
9
10 We observed in the 3 overwintering seasons a greater spread in the timing of life-history
11 transition. Planting 1 was started in early December and no germination occurred
12 before spring. Although the precise germination date was not scored for the first
13 planting, we observed that germination was staggered across 1 month. This observation
14 was repeated for planting 5, where germination occurred after 2-3 months (Suppl.
15 Fig.3). For both of these plantings, the date of germination had no impact on the date of
16 flowering: all plants flowered within a week. Our experiment also included another fall
17 planting (planting 3), which displayed germination staggered between 10 and 40 days
18 after seed dispersal. In this planting, the C24 background flowered within a 20-day
19 window (60 to 80 days) in late fall, at a time where the Col-0 background continued
20 vegetative growth. By contrast, the Col-0 background flowered in spring, within a large
21 80-day window (Suppl. Fig. 3). This spread in the average timing of flowering was
22 observed only in planting 3, the only planting where the two genomic backgrounds
23 showed a significant difference in development (Suppl. Fig. 3).
24
25

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1
2
3 **Discussion**

4 In this study, we designed a field experiment to quantify the fitness outcome of climate,
5 substrate and genotypic variation on expressed phenotypes and associating fitness
6 levels in a natural setting. Our results reveal that environmental variance experienced
7 over successive growth seasons at a given locality of intermediate latitude is not
8 buffered by phenotypic plasticity. Genotypic differences in phenotype and fitness
9 fluctuate in magnitude across soil conditions and seasons. Seasonal fluctuations
10 experienced at intermediate latitude markedly alter expressed life cycles.
11

12 **Seasonal fluctuations in the life cycles expressed by a single genotype**

13 The performance of various *A. thaliana* genotypes in the field has already been reported
14 in several studies [20,21,23,27], but our experiment is the first to monitor the life cycle
15 dynamics naturally deployed by single genotypes. This experiment was conducted along
16 5 consecutive seasons and included two summer plantings and three fall plantings. From
17 the second season onward, the date of planting was determined by the date of fruit
18 maturation in the field, and the date of germination was determined by the level of
19 dormancy imposed in the field during and after seed maturation. The genotypes were
20 thus allowed to express their natural life cycle. At the temperate latitude of our
21 experimental site, we show that *A. thaliana* completes two cycles per year while the
22 third one is suspended during winter, either at the rosette (planting 3) or at the seed
23 stage (planting 5). Our experiment shows that a given genotype may manifest diverse
24 life cycles in the course of successive seasons, confirming theoretical predictions based
25 on a combination of hydrothermal and photothermal models of germination and

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1 flowering decisions[33]. The life stage at which the winter interruption occurred
2 seemed to depend on the timing at which the second generation was finished, either
3 because of variation in the maternally imposed dormancy, the adverse conditions for
4 germination, or possibly the onset of secondary dormancy triggered by low
5 temperatures [34-36].
6 We further observed that life time fruit production also varied by up to 36-fold across
7 successive seasons. This is likely to be due to the dramatic environmental differences to
8 which genotypes are exposed throughout the successive seasons. Indeed, level of
9 fluctuation for a winter annual cycle replicated over 5 distinct years reported up to 7-
10 fold fitness fluctuations [21]. Because overwintering generations tended to reach higher
11 fitness than summer generations, we can further conclude that, at the latitude where
12 this experiment was conducted, variation in characters important for winter survival
13 may be comparatively more crucial for adaptation than those important for completing
14 a life cycle in summer. Nevertheless, since we also observed that the life-history stage of
15 overwintering could change across years, the traits exposed to winter selective
16 pressures also likely fluctuate.
17
18 **Seasonal fluctuation in expressed life history differences between genotypes**
19 Based on previous laboratory studies, we expected that the two backgrounds would
20 display markedly different life histories in the field. The genotype C24 was reported to
21 flower 11 days after Col-0 in long day conditions but is a relatively early genotype under
22 short day conditions because of a weak FLC allele [30]. In addition, high ambient
23 temperature (27-30°C) triggers faster flowering in Col-0, but delays flowering in C24,
24 whereas C24 seeds matured under long day conditions at 20°C showed 2 weeks longer
25 primary dormancy than Col-0 (JDM, pers. com.).

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1
2 Life history decisions such as germination and flowering time are known to be
3 dependent on the environment [27,33,37-39]. Here, we show that phenotypic
4 differences between genotypes can be either masked or exposed across the successive
5 life cycles of a natural setting. Indeed, a major difference in the timing of flowering of
6 Col-0 and C24 was observed only when seeds were sown at the end of August. The late
7 summer time window has been demonstrated to impact the manifestation of flowering
8 time differences controlled by the vernalization pathway [37].
9

10 **The Col-0 genotype appears better adapted to the experimental site**

11 The relative fitness of the Col-0 and C24 backgrounds were reported to change markedly
12 across geographical sites [23]. The Col-0 genotype produced 50% more siliques in Halle,
13 Germany, but its fitness was 12% of that of C24 in Norwich, UK, while both genotypes
14 showed comparable fitness in Valencia, Spain [23]. In our experiment, the Col-0
15 background generally displayed higher fitness than C24 despite temporal seasonal
16 fluctuations. This suggests that it is generally well adapted to the climatic conditions of
17 our field. Its genome is assigned to a Western European *A. thaliana* clade of genotypes
18 originating from natural stands in Germany [29]. The magnitude of the fitness difference
19 nevertheless changed markedly across soil conditions and seasons. A recent study
20 reported that *A. thaliana* genotypes originating from Southern latitudes, which is the
21 case for C24, perform comparatively well at intermediate temperate latitudes [40]. C24,
22 however, did not perform better than Col-0 even in sand where water limitations might
23 have provided it with an advantage. In fact, the Col-0 genotype performed better than
24 C24 in sand, even though plants suffered a 3-week long period of high temperature
25 without precipitation in planting 2 (Fig.1, Fig. 3). Yet, we also observed that micro-

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1 geographic heterogeneity in substrate, which is commonly found in natural *A. thaliana*
2 stands, can magnify or mask differences observed between Col-0 and the Southern
3 genomic background C24 (Fig. 3B).
4

5 **Rare but radical events counter select inappropriate flowering time**

6 The evolution of gene frequencies in natural populations depends on differential fitness,
7 and therefore on the environmental factors that promote or buffer the expression of this
8 variation[11]. Our experiment shows that although phenotypic differences in the timing
9 of flowering are masked in 3 of 4 seasons, their expression coincided with a severe
10 selection against the early flowering genotype. Flowering however occurred over a
11 broader time window in this planting and a couple of populations (pots) in which a
12 handful C24 individuals which had not flowered, were nevertheless able to regenerate
13 their rosettes and complete their cycle. The transition to flowering might thus have
14 caused the plants' vulnerability to low temperatures. This experiment therefore depicts
15 relatively rare but radical selective events by which genotypes flowering early in short
16 days might have been counter-selected in regions with sometime severe winter
17 conditions. Such an ecological scenario may explain why local adaptation remains
18 pervasive in this species despite the seasonal fluctuations affecting the expression of
19 adaptive phenotypes that we document [20,23].
20

21 **Temporal fluctuations of allelic effects on fitness**

22 Our experiment further shows that seasonal and environmental fluctuations must be
23 taken into account when studying the genomic underpinnings of local adaptation.
24 Extrapolating the evolutionary trajectory of mutations based on their impact on
25 ecological performance in a reductive experimental setting is not directly possible.

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1 Whereas the Col-0 background generally performed better over the whole experiment,
2 the Chromosome 4 fragment had effects of changing signs in a small subset of
3 conditions. This small region, which only contains about 10% of previously reported
4 fitness-relevant differences across the geographical range of the species, can have, in
5 some conditions, an effect comparable to that of the genomic background. In fact,
6 interactions between genetic and temporal variation are probably more the rule than
7 the exception. As an example, variation in both plant density and water supply, two
8 environmental factors that are likely to fluctuate over time, has been recently shown to
9 change the effect of a polymorphism impacting water-use efficiency in *A. thaliana* [41].
10
11 **Conclusion**
12 The current development of faster and cheaper sequencing methods boosts our ability
13 to investigate the basis of local adaptation in a number of plant species, including rare
14 endemics or aggressive invasive species [42,43]. Annotating how functions encoded in
15 the genome impact ecological performance and fitness seems within reach [44]. Our
16 findings, however, has important bearings for our conception of the specific challenges
17 we are facing for plant (or animal) species that can shift their temporal niches across
18 generations. The likelihood that given genotypes meet the seasonal window where their
19 selective advantage can be exposed will have to be characterized. For this, the genotypic
20 specificities of plastic life history regulation (as e.g. in [45]), the temporal environmental
21 variance, and the scale and impact of micro-geographic substrate heterogeneity will
22 have to be jointly evaluated.
23
24 **Acknowledgements:** We thank Hildegard Schwitte for her help in quantifying fitness in
25 the 4th and 5th plantings. This research was supported by the Deutsche Forschung

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3 available upon request.

4

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1

2 **Tables**

	F (df num, df denom)	Pr(>F)	
Plant Density	51.3494 (1 , 266)	1.03E-11	***
Soil Composition	21.446 (1 , 265)	6.08E-06	***
Genomic background	47.5303 (1 , 264)	5.12E-11	***
Planting	119.0384 (4 , 260)	2.20E-16	***
Chr4 Genotype	1.7507 (1 , 259)	0.1871	
Soil Composition:Genomic background	37.8494 (1 , 258)	3.34E-09	***
Soil Composition:Planting	7.5266 (4 , 254)	1.03E-05	***
Genomic background:Planting	80.7008 (3 , 251)	2.20E-16	***
Planting:Chr4 Genotype	3.1259 (4 , 247)	0.01573	*
Soil Composition:Genomic background:Planting	3.6438 (3 , 244)	0.01344	*
Genomic background:Planting:Chr4 Genotype	2.8582 (4 , 240)	0.02433	*
Soil Composition:Genomic background:Planting:Chr4 Genotype	10.4293 (9 , 231)	1.67E-13	***

3

4 Table 1: Summary of the deviance table for the minimal generalized linear model testing the
5 effect of planting, soil composition, genomic background and their interaction on lifetime
6 silique productions. Non significant interaction terms were removed sequentially following
7 Crawley 2005. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Dispersion parameter
8 for Negative Binomial (r=2) family taken to be 0.8980737. Residual deviance: 227.57 for 231
9 degrees of freedom. GLM final formula: (silinb + 1) ~ Plant Density + Soil Composition +
10 Planting + Genomic background + Chr4 Genotype + Soil Composition:Planting + Soil
11 Composition:Genomic background + Planting:Genomic background + Planting:Chr4
12 Genotype + Soil Composition:Planting:Genomic background + Planting:Genomic
13 background:Chr4 Genotype + Soil Composition:Planting:Genomic background:Chr4
14 Genotype.

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	F (df num, df denom)		Pr(>F)	
Plant Density	43.4516	(1 , 184)	5.25E-10	***
Soil Composition	45.9537	(1 , 183)	1.91E-10	***
Planting	169.4389	(4 , 179)	2.20E-16	***
Chr4 Genotype	0.4167	(1 , 178)	0.519465	
Soil Composition:Planting	4.7902	(4 , 174)	0.001097	**
Planting:Chr4 Genotype	3.1058	(4 , 170)	0.016909	*

Table 2: Summary of the deviance table for the minimal generalized linear model testing the effect of planting, soil composition and their interaction on lifetime silique productions of plants with a Col-0 genomic background. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 – Residual deviance: 172.56 for 170 degrees of freedom. Dispersion parameter for Negative Binomial (r = 2.8) family taken to be 0.94596. GLM final formula: formula = (silique number + 1) ~ Plant density + Soil Composition + Planting + Chr4 Genotype + Soil Composition: Planting + Planting: Chr4 Genotype

	Estimate	Std.	Error	t-value	
(Intercept C24 - Sand)	4.22497	0.17202	24.561	2.00E-16	***
Plant Density	-0.05356	0.0085	-6.301	3.59E-09	***
Soil Composition (Turf)	1.11207	0.15662	7.1	5.73E-11	***
Genomic background Col-0	0.8567	0.15614	5.487	1.86E-07	***
Planting 2	0.76139	0.18514	4.113	6.64E-05	***
Planting 4	0.99733	0.16981	5.873	2.97E-08	***
Chr4 Genotypes	-0.46511	0.19556	-2.378	0.018739	*
Soil Composition Turf:Genomic background Col-0	-0.89446	0.19493	-4.589	9.82E-06	***
Planting 2:Chr4 Genotypes	0.91126	0.24851	3.667	0.000348	***
Planting 4:Chr4 Genotypes	0.36777	0.23685	1.553	0.122741	

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1 Table 3: Coefficient estimates for minimal generalized linear model after sequential removal
2 of non significant interaction terms performed on lifetime fruit production (silique number) in
3 planting 1, 2, 4, where both genomic backgrounds survived and reproduced. Signif. codes: 0
4 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 (Dispersion parameter for Negative Binomial (r = 2.9)
5 family taken to be 0.8304712).
6

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1

2 **Fig. legends**

3 **Fig. 1:** Time plan of the field experiments along five consecutive life-cycles and local
4 meteorological conditions. Meteorological parameters were retrieved from the nearby
5 weather station at airport Nörvenich. Relative air humidity is shown in blue, maximum
6 day temperature in red, minimum day temperature in pink and average day temperatue
7 in orange. Black arrows on the lower panels mark the starting date of each planting.
8 Gray boxes mark the duration of each planting. White, green, red and orange rectangles
9 stand for winter, spring, summer and fall, respectively. Blue and green arrows mark the
10 approximate germination and flowering time, respectively. C24 and Col-0 had different
11 flowering times only at planting 3.

12

13 **Fig. 2:** Distribution of total fruit number as a function of planting, quantified as
14 ln(number of fruits +1). A- For individual with the C24 genomic background only, B- For
15 individual with the Col-0 genomic background only. Letters designate significantly
16 different plantings, at p=0.01.

17

18 **Fig. 3:** A- The effect of soil on fruit production -transformed as ln(x+1)- changes across
19 generations. In generation 3, plants grown on sand produce significantly more siliques
20 (Fold change=14, p= 0.0007). B- Focusing on planting 1, 2 and 4, where both genomic
21 background survived, reveals that the Col-0 genomic background performs better on
22 sand, whereas growth on turf did not cause strong differences in silique production.
23 ***mark p-values for the subset of conditions where substrate or genomic background
24 had a significant impact on plant performance.

25

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1 **Fig. 4:** Total fruit number -transformed as ln(x+1)- depends on Chr4 introgression in 3
2 of 16 combinations of three factors (genome, substrate and planting). *p and FC: p—
3 value and fold-change attributed to the C24 chromosome 4 allele within the factor
4 combination.
5
6
7 **Fig. 5:** Life time fruit production -transformed as ln(x+1)- as a function of the number of
8 days to flowering in sand and turf. A- Data partitioned by plantings, B- data partitioned
9 by genomic background.
10
11 **Supplemental Figures**
12 **Suppl. Fig. 1:** Photograph of the field experimental set up.
13 **Suppl.. Fig. 2:** A. The effect of plant density in the pot was only strong in planting 2, 3
14 and 5. For 3 and 5, Co-0 was the only genomic background that survived. B. For planting
15 2, the C24 background did not perform well, so that density was too low to reveal an
16 impact of competition on total life time fitness.
17 **Suppl. Fig. 3:** Relationship between days to flowering (DTF) and days to germination
18 (DTG) in each planting for each genomic background. Plantings 2 and 4 had similar
19 germination and flowering time. By contrast, generation 3 showed spread flowering
20 time and generation 5 rather spread germination (spring germination), suggesting that
21 the buffering of germination and flowering differed across planting (and across
22 genotypes). Note that the Chr4 introgression did not impact these differences. In
23 generation 1, the date of germination was not scored, but three cohorts were observed,
24 reflecting a spread of germination over March/April, whereas flowering time occurred
25 within 1-2 weeks.

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30

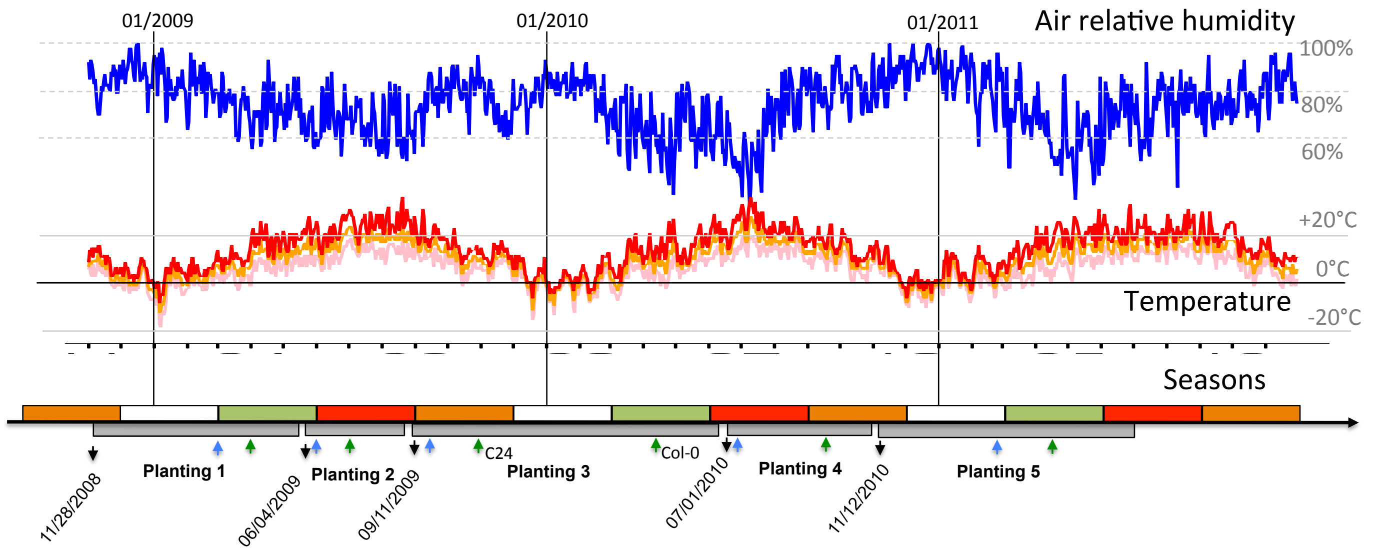

Figure 1: Time plan of the field experiments along five consecutive life-cycles and local meteorological conditions. Meteorological parameters were retrieved from the nearby weather station at airport Nörvenich. Relative air humidity is shown in blue, maximum day temperature in red, minimum day temperature in pink and average day temperatue in orange. Black arrows on the lower panels mark the starting date of each planting. Gray boxes mark the duration of each planting. White, green, red and orange rectangles stand for winter, spring, summer and fall, respectively. Blue and green arrows mark the approximate germination and flowering time, respectively. C24 and Col-0 had different flowering times only at planting 3.

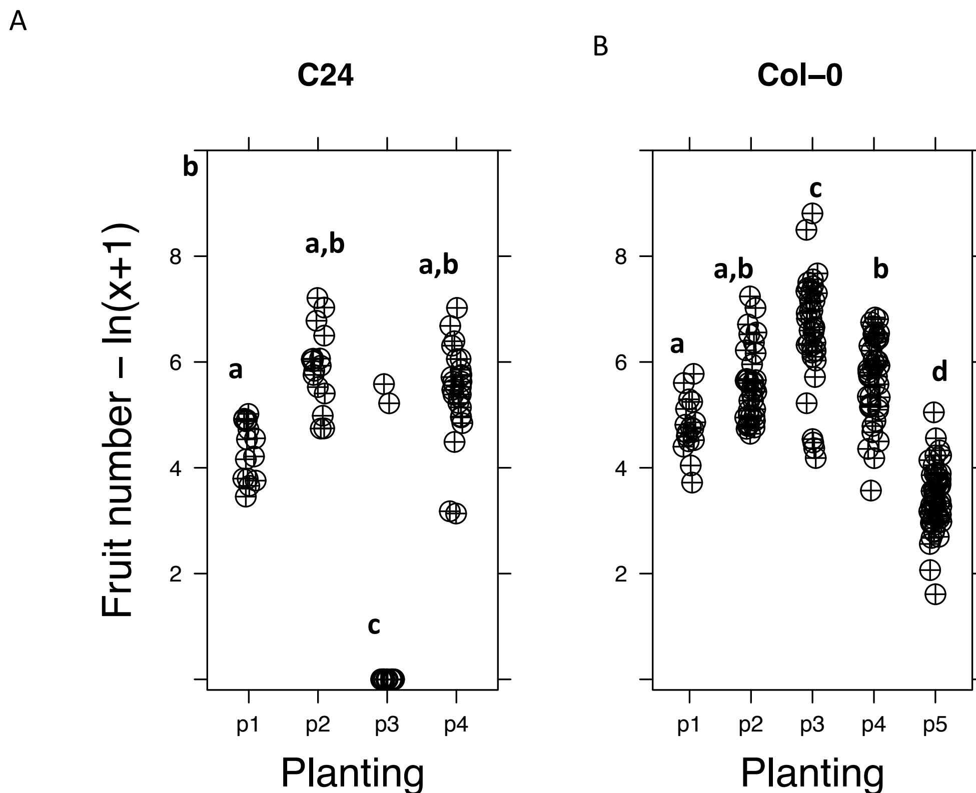

Figure 2: Distribution of total fruit number as a function of planting, quantified as ln(number of fruits +1). A- For individual with the C24 genomic background only, B- For individual with the Col-0 genomic background only. Letters designate significantly different plantings, at *p*=0.01.

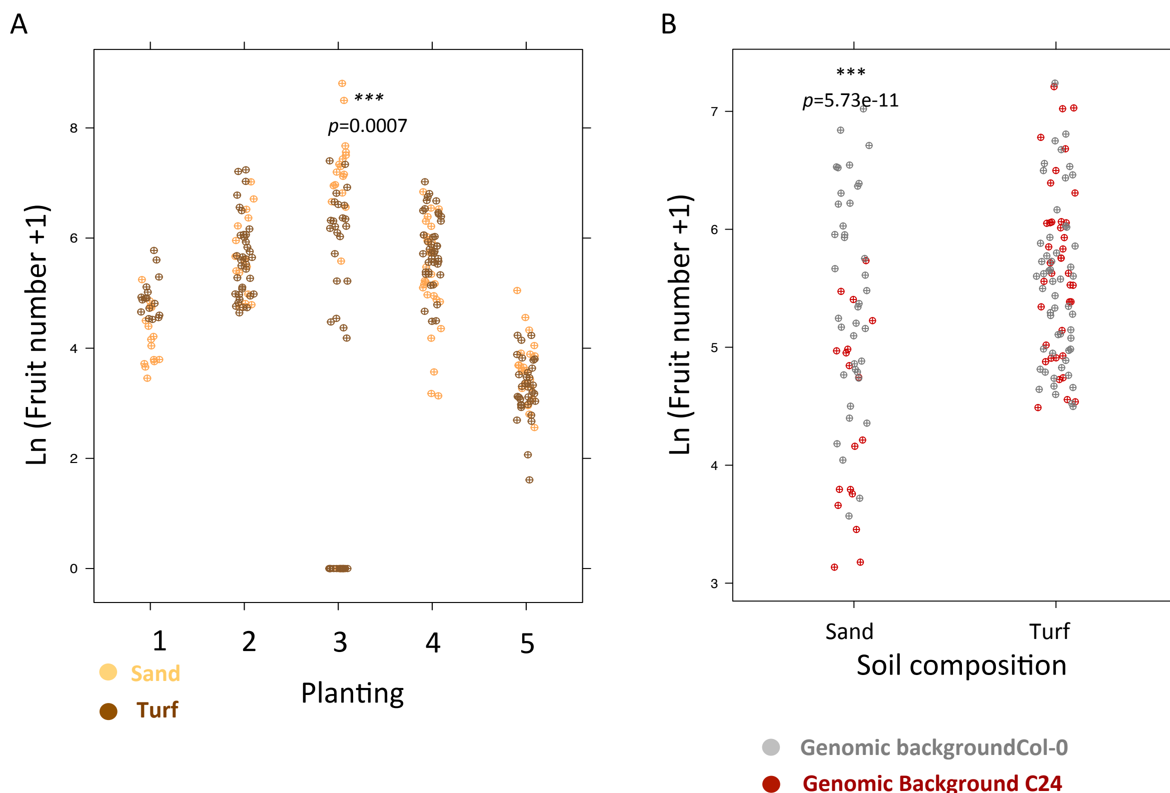

Figure 3: A- The effect of soil on fruit production-transformed as ln(x+1)- changes across generations. In generation 3, plants grown on sand produce significantly more siliques. B- Focusing on planting 1, 2 and 4, where both genetic background survived, reveals that the Col-0 genetic background performs better on sand, whereas growth on turf did not cause strong differences in silique production. ***mark p-values for the subset of conditions where substrate or genomic background had a significant impact onplant performance.

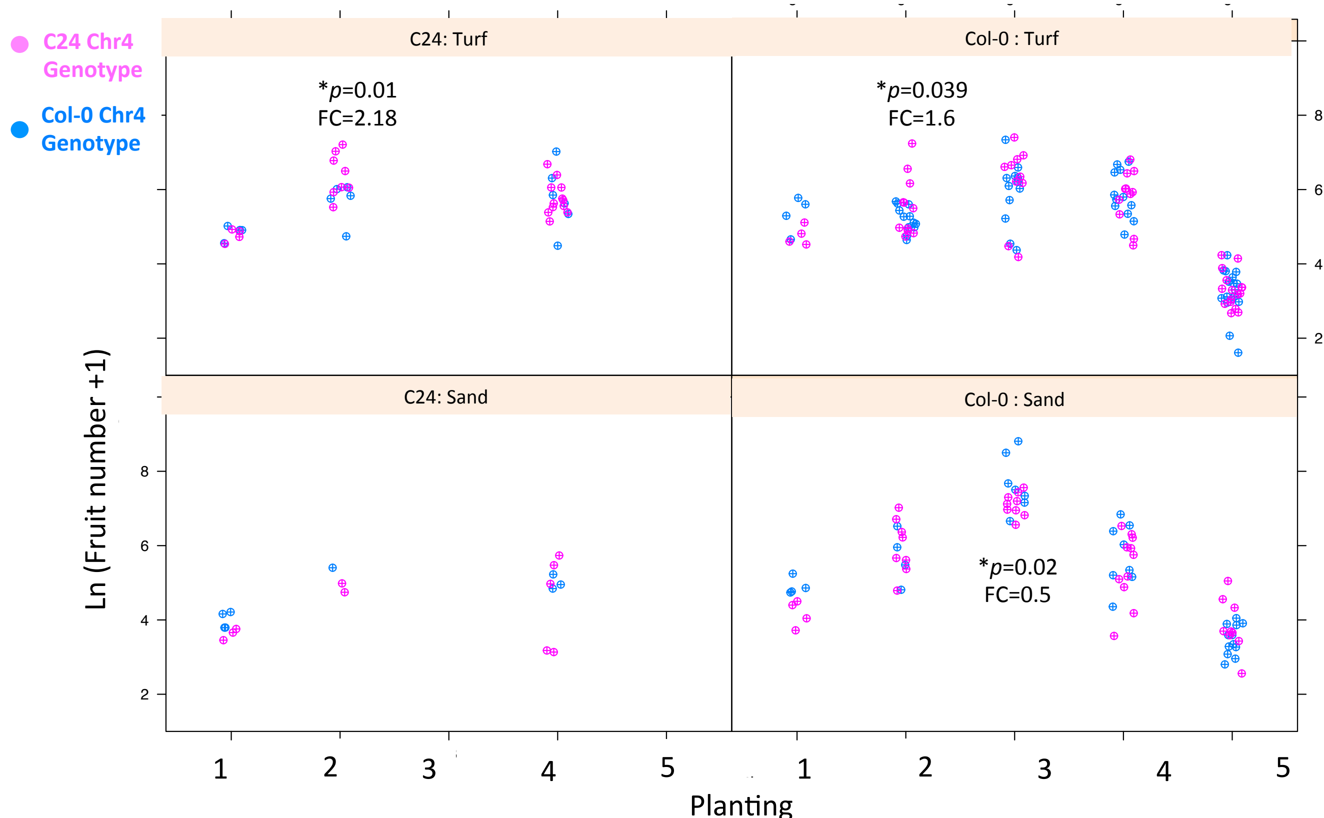

Figure 4: Total fruit number -transformed as ln(x+1)- depends on Chr4 introgression in 3 of 16 combinations of three factors (genome, substrate and planting). *p and FC: p—value and fold-change attributed to the C24 chromosome 4 allele within the factor combination.

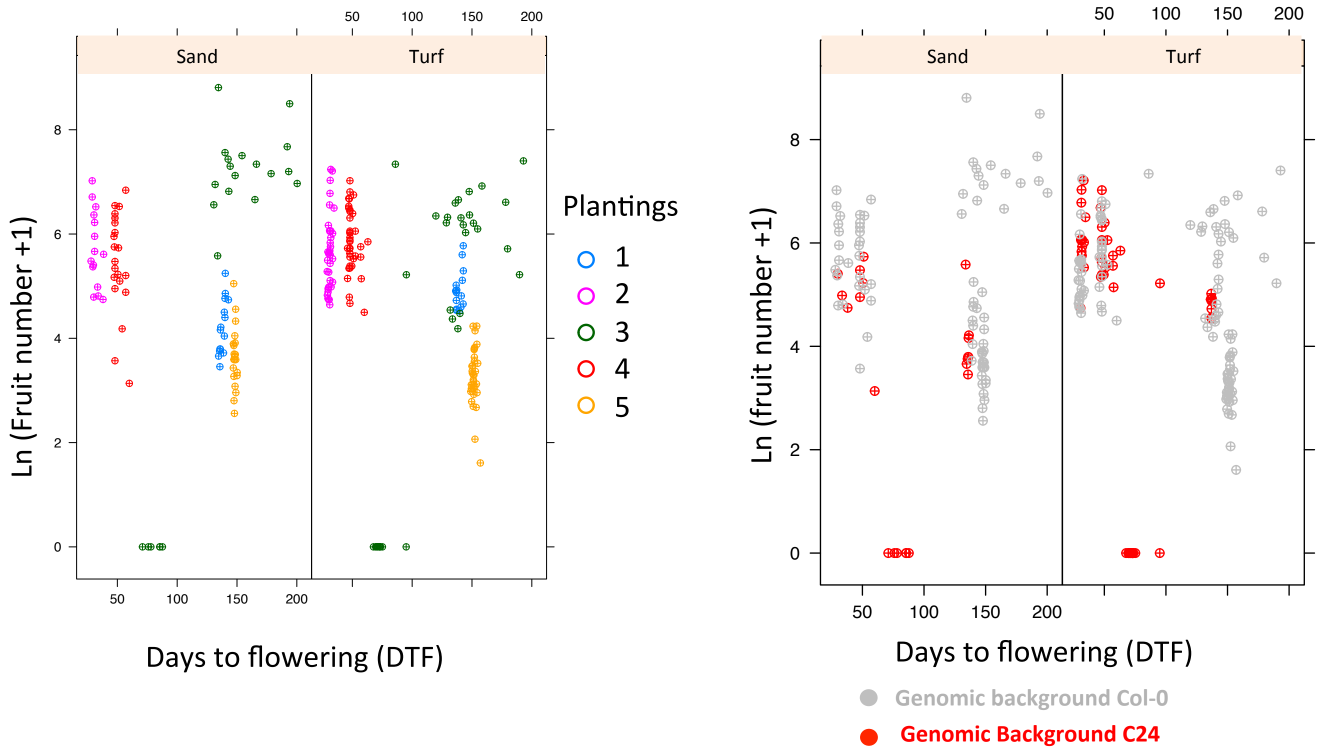

Figure 5: Life time fruit production -transformed as ln(x+1)- as a function of the number of days to flowering in sand and turf. A- Data partitioned by plantings, B- data partitioned by genomic background.