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2 Local *Populus fremontii* genotypes outperformed by transplants: re-examining the home-
3 site hypothesis in restoration
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1
2 **Abstract.** We examined the hypotheses that individual plant genotype and source
3 population of Fremont cottonwood, *Populus fremontii*, would have a significant effect on
4 the survival of trees in a 6,000 tree restoration site at Cibola National Wildlife Refuge,
5 AZ. Experimental examination of genotypic effects is important because standard
6 restoration practices advocate the use of local genotypes, but tests are rarely conducted to
7 quantify genetic effects and to determine if genotypes derived from local populations
8 actually perform better than genotypes from more distant source populations. Several
9 major patterns emerged. 1. Genetic effects were large; mean mortality rate among
10 genotypes ranged from 9.84% to 88.89%. 2. Environmental and/or maternal effects were
11 not significant (i.e., planting micro-location, sapling diameter, or sapling height).
12 Genotype was a significant factor in determining mortality ($p < 0.001$), explaining 11.26
13 % of the variation among genotypes. 3. Surprisingly, local genotypes performed
14 significantly worse than genotypes from much farther away (up to 900km). Significant
15 single variable relationships were found between mortality and geographic distance from
16 site of origin ($r^2 = 0.33$), elevation of site of origin ($r^2 = 0.33$), mean annual precipitation
17 of site of origin ($r^2 = 0.28$), and mean annual temperature of site of origin ($r^2 = 0.29$). In
18 combination, these results show that mortality rates generally decrease with increasing
19 distance from the restoration site. These results have significant implications for
20 restoration efforts as they do not support the concept of a 'home site advantage' (Montalvo
21 and Ellstrand 2000). They suggest that climate change and other anthropogenic effects
22 on the environment (i.e., altered hydrological and salinity regimes due to flood control
23 and agricultural practices) may have shifted the local environment so much that local
24 genotypes are no longer best adapted to local conditions. By selecting specific genotypes

1 for specific locations, it may be possible to lower mortality rates, thus increasing
2 restoration efficiency. We view our findings as a major conundrum for restoration efforts
3 and have initiated further studies to experimentally examine this initial study that should
4 be cautiously interpreted, but nevertheless may be an important warning that
5 anthropogenic-based environmental changes may so alter environments that the strategies
6 of restoration programs need re-evaluation.

7 Keywords: common garden, ecological genetics, Fremont cottonwood, home site
8 advantage, mortality, *Populus fremontii*, restoration

9

10 **Introduction**

11 Restoration efforts should focus on selecting particular genotypes, rather than
12 locally adapted stock, in order to more effectively restore habitat. Understanding the
13 role genetics play in influencing survival of individuals is important, as locally adapted
14 stock may underperform in the face of climate change and other anthropogenic factors
15 that are altering ecosystems more quickly than local populations can adapt. Riparian
16 habitat along the lower Colorado river has declined from 90,000 acres in 1938 to 6,000
17 acres in 1998 due to anthropogenic factors (Cohn 2001). Recently, multiple public and
18 private agencies have been involved in the active restoration of the lower Colorado River
19 Basin. The Bureau of Reclamation in particular has set out a goal of restoring 10,000
20 acres of riparian forest by 2014. With such extensive restoration efforts, the genetic
21 composition of the stock may have an important and long-lasting impact on future
22 riparian forests in the southwestern U.S.

1 Other studies have examined how distinct genetic populations within a species
2 (ecotypes) influence persistence and genetic composition of populations. Introduced
3 ecotypes within genetically different populations vary in persistence and compositional
4 effects. Some studies have found total dominance by introduced ecotypes (“swamping”)
5 (Hufford and Mazer 2003). For example, a European version of the grass *Phragmites*
6 *australis* (common reed) was found to rapidly overtake an American ecotype of *P.*
7 *australis* (Saltonstall 2002). Others found greater persistence of locally adapted ecotypes
8 in a home-site when compared to non-native stock. Montalvo and Ellstrand (2000) found
9 that *Lotus scoparius* (deerweed) decreased in persistence as distance from its homesite
10 increased.

11 Although some of the above studies strongly agree for the use of local stock in
12 restoration plantings, climate change represents an unknown ‘wild card’ for conservation
13 and restoration. For example, the most recent IPCC report (IPCC 2007) shows that the
14 American Southwest has undergone and is predicted to show the greatest climatic
15 changes of the 48 contiguous states. In the last 50 years the growing season has increased
16 by about 27 days and an ongoing drought since 1996 has resulted in major vegetation
17 changes. For example, foundation species (ponderosa pine, pinyon pine, aspen,
18 manzanita, cottonwood) from alpine forests to desert and riparian habitats have recently
19 suffered regional mortality rates of 15-41% (Gitlin et al. 2006). As these species are
20 foundation species and some, such as cottonwoods characterize rare habitat types that are
21 hotspots of biodiversity, the community and ecosystem consequences are likely to be
22 great (see also Parmesan 2006). These findings are supported with other studies of high
23 mortality throughout the region (e.g., Allen and Breshears 1998, Breshears et al. 2005,

1 Mueller et al. 2005) and modeling of climatic envelopes predict grim consequences for
2 many of these species. For example, modeling by Rehfeldt et al. (2006), suggest that one
3 of the most common species in Arizona, pinyon pine (*Pinus edulis*) may be extirpated
4 from the state by 2090. Similarly, modeling by Gitlin and Whitham (in review) argues
5 that cottonwoods are likely to disappear from the lower Colorado River, which includes
6 the study site of our current paper

7 Genetics have been found to influence leaf size, chlorophyll concentration, and
8 leaf mass and multiple community and ecosystem traits in *Populus* forests of the
9 southwest (Rowland 2001, Whitham et al. 2006). Understanding how genetic and
10 environmental factors(including homesite distance) interact with the planting of native
11 and non-native ecotypes determines how restoration efforts may be affected.

12 In restoration projects, as in natural regeneration, early sapling mortality
13 maydefine the character of mature forests through the effects of selection. Those saplings
14 that survive the early stages of restoration have the highest potential to influence the
15 community and ecosystem in the long-run, while those that fare poorly are less likely to
16 maintain further ecosystem-level influence. Because genetic differences can affect early
17 survival of out-planted saplings, restoration efforts may be unintentioned experiments,
18 where only the genetic stock best fit for early survival will be selected to influence the
19 future ecosystem.

20 We addressed two major hypotheses. First, extensive genetic variation in Fremont
21 cottonwood would be reflected in significantly different mortality rates across genotypes.
22 Second, local genotypes should perform better than genotypes derived from populations
23 farther away from our planting site, i.e., the ‘home site advantage’(Montalvo and

1 Ellstrand 2000). Answers to these questions are important because they affect our
2 understanding of basic ecological and evolutionary principles, which have important
3 implications for environmental restoration.

4

5 **Methods**

6 **Study Site**

7 Data were collected from three established experimental restoration plots in the
8 Cibola National Wildlife Refuge in southwestern Arizona. The common garden is
9 organized with 16 distinct genotypes of *P.fremontii* randomly transplanted into three
10 plots. The saplings used in the study were propagated cuttings from 16 sites across the
11 southwestern United States (fig. 1). Cuttings were taken before leaf-out, from January to
12 April of 2005 and rooted in a greenhouse for 6 months before transplanting. Each plot
13 was organized in a 16 by 20 grid (320 saplings), with 3 meters between each transplant.
14 Plots were subdivided into twenty 4 by 4 blocks (16 saplings), each containing 1, 2, 4, 8,
15 or 16 varieties, respectively. To account for possible variation in field conditions, the
16 site was laser-leveled and is regularly flood-irrigated.

17

18 **Sampling Methods**

19 Sapling mortality was examined six months after transplant. There were 17 *P.*
20 *fremontii* that could not be located (out of 960 total), and were not factored into the final
21 sample size. Genotype, mortality, height, and stem diameter data were collected for each
22 sapling. Height was measured from base to highest apical meristem, while stem diameter
23 was measured at the base of each sapling. Mortality was gauged by assessing whether

1 chlorophyll was present in the stem by removing a small piece of bark near the base and
2 checking for green pigmentation. To account for any potential effects that environmental
3 factors might have on the fitness of each genotype, a number of variables were
4 obtained from each home-site. Data compiled included geographic distance, latitude,
5 elevation, and annual means of both temperature and precipitation. Geographic distance
6 and latitude were obtained using GIS coordinates. Elevation was recorded at the
7 time when each cutting was taken (Table 1). Long term temperature and precipitation
8 averages were taken from the Western Regional Climate Center
9 (<http://www.wrcc.dri.edu/CLIMATEDATA.html>). Data from the closest weather station
10 to each home-site was used.

11

12 **Statistical Methods**

13 Average mortality was calculated for each genotype. An analysis of variance was
14 run using SPSS 13.1 for Windows (SPSS Inc, Chicago, IL USA) to determine
15 significance ($p \leq 0.05$) of mortality rates between genotypes. We used linear regressions
16 to examine relationships between each continuous variable and mortality. Broad sense
17 heritability, the ratio of variance between genotypes, was also calculated using standard
18 methods (Bailey et al. 2006). We were unable to directly compare genotype and
19 environmental variables of the homesite since a single genotype was propagated from
20 each homesite independently.

21 To determine the relative influence of co-varying environmental factors on
22 sapling mortality we used a model selection approach that allows ranking of multiple
23 predictive models based on information-theoretic criteria (Burnham and Anderson 2002).

1 This approach avoids the pitfalls of other model selection techniques such as stepwise
2 regression which may have unreasonable assumptions, or preferentially pick models
3 based on order of inspection (Burnham and Anderson 2002).

4 Briefly, the information-theoretic approach uses maximum likelihood theory and
5 the principle of parsimony to assess the strength of evidence for each model in a
6 candidate set of a priori defined models. We used Akaike's Information Criterion,
7 adjusted for small sample size (AICc), an estimate of model likelihood, Akaike weights
8 (w_i), and an evidence ratio computed from these variables, to simultaneously compare
9 and rank multiple models from a set of a priori candidate models (see Burnham &
10 Anderson, 2002). Each measure provides an index of the best model given the data, and
11 the evidence ratio gives a comparative "odds" of the top-ranked model being the best
12 model given the data. All models were single variable linear models due to low sample
13 sizes. The models included "altitude of homesite," "temperature of homesite,"
14 "precipitation of homesite," "basal diameter of sapling," and an "intercept-only" model).
15 Models whose ΔAIC (AICc relativized to the lowest value) differed by less than 2.0 were
16 not considered statistically distinguishable, as is common practice (Burnham &
17 Anderson, 2002). The AIC_c values were calculated from AIC values given in JMP
18 stepwise regression analyses (JMP Discovery statistical package 4.0, SAS Institute Inc.,
19 Cary, NC, USA),

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21 **Results**

1 As predicted, we found a significant difference in mean mortality rates between
2 genotypes ($p < 0.001$). Average mortality ranged from 9.84% to 88.89% (Fig. 2). The
3 average mortality rate for all transplants studied was 31.55%.

4 Although elevation and environmental factors were significant predictors of
5 mortality, highest mortality occurred among genotypes from areas proximal to the
6 restoration site, and lowest mortality occurred in genotypes from distant, higher
7 elevations, with lower average temperatures and higher annual precipitation (**Figure 3**).
8 There were significant negative linear relationships between mortality and geographic
9 distance from homesite (where cuttings originated; $p < 0.001$), elevation of homesite ($p <$
10 0.001), and mean annual precipitation of homesite ($p < 0.001$). A significant positive
11 relationship was found between mortality and mean annual temperature of homesite ($p <$
12 0.001).

13 Although we found elevation to be the best ranked model for predicting mortality
14 according to our model selection criteria, it was indistinguishable from mean annual
15 temperature and precipitation. The elevation model best predicted mortality according to
16 all model selection criteria, including: the ΔAIC_c values (lowest), the likelihood value for
17 the best model (LIKELIHOOD; 1.0), the Akaike weight of evidence (w_i ; closest to 1),
18 and the evidence ratio (EVID. RATIO; next best model has a 1:1.5 chance of being
19 better, given the data). This is reflected by the delta AIC_c which suggests this model is
20 statistically indistinguishable from the next three. The size of the cutting (diameter) is a
21 far worse predictor of mortality than the the cutting's origin .

22 Some variation in planting conditions existed in the common garden, but neither
23 location nor sapling size were significant predictors of mortality. We found no significant

1 correlation between mortality and plant height ($p = 0.184$), basal diameter of sapling ($p =$
2 0.957), or orientation in the garden (east-west: $p = 0.056$; north-south: $p = 0.153$).

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5 **Discussion**

6 In a restoration context, genotypic variation in early sapling mortality can affect
7 project efficacy dramatically. In phreatophytic and facultatively phreatophytic (see Cox
8 et al. 2005) species such as *P.fremontii*, early sapling survival may help determine
9 whether individuals live long enough to make contact with the water table, ensuring later-
10 year survival (Amlin and Rood 2002). This study shows high variation in mortality
11 among genotypes in a common garden. Mortality rates ranged from 88.89% in a
12 genotype from the Hassayampa Preserve, AZ (HP), to 9.84% in a genotype from the
13 Weber River, UT (B161). Calculation of broad sense heritability suggests that 11.26% of
14 mortality rates may be attributed to differences among genotype. While this difference is
15 small, it is significant enough to be useful in silvicultural and restoration applications.
16 For example, in agricultural applications, a H^2_b of greater than XXX is frequently
17 exploited for breeding purposes.

18 The results of this study suggest that temperature, elevation, and precipitation of
19 home-site are all effective predictors of *P. fremontii* sapling persistence in restoration
20 efforts. However, the results of these relationships run counter to our expectations. We
21 hypothesized that mortality would increase with increasing home-site distance from the
22 location of the restoration site. Home-site climatic variables that were more similar to the
23 restoration site's environmental variables would predict survival of out-planted saplings.

1 We found the reverse pattern, where as geographic distance of home-site, and
2 precipitation increased, mortality rates generally decreased.

3 In contrast to our own expectations and the previous data of other researchers
4 (Montalvo and Ellstrand 2000), these results suggest that locally planted stock may not
5 always be the best adapted to local conditions. In an evolutionary context, this may be
6 due to inbreeding or changing environmental conditions. Locally planted stock that does
7 not receive new genetic material may be at risk when environmental and climate factors
8 change, and locally adapted stock populations are greatly reduced, rather than molded by
9 selection pressures. Because correlation does not necessitate causation, we suggest
10 multiple explanations for this pattern: 1) phenological differences (e.g., length of winter
11 dormancy) associated with climatic differences in environments provides for a higher
12 regeneration success in the field. Differences in collection techniques and timing may
13 have contributed similarly to these differences; 2); flood irrigation of out-planted saplings
14 creates an environment advantageous to saplings from northern, moister climates where
15 trees are in constant contact with a water-table 3) the correlation arises from a correlation
16 with another variable that we did not measure that co-varies with elevation and
17 precipitation; 4) by sampling from a larger and potentially more diverse genetic pool (in
18 more northern or higher elevation climes), survival rates may increase relative to smaller
19 gene pools due to sampling effect; and finally 5) susceptibility to local pathogens by local
20 stock increases their mortality relative to distant genotypes which may not have as many
21 locally adapted pests and pathogens due to high genetic specificity of fungal and
22 arthropod communities(Whitham et al. 2006). This last explanation is identical to the
23 argument often used at the species level to explain success of exotic species.

1 All cuttings were collected using the same methodology and grown to leaf-out
2 and then induced into dormancy in a greenhouse before planting. However some lower
3 latitude trees have only brief dormancy periods, and so dormancy of cuttings at time of
4 collection could not be ensured in all cases. Because some trees may have not been
5 completely dormant at time of collection, those trees may have stored fewer resources,
6 and may have been less prepared for out-planting. However, this may be a perpetual
7 pattern with cuttings taken from lower elevation warmer climates. More northern
8 locations may have more complete dormancy, making cutting propagation more
9 successful in restoration attempts. This could have important implications for large
10 restoration plantings where low mortality is important, re-planting of dead trees is
11 unrealistic, and managers must balance tree survival with a desire to plant local stock.

12 Previous studies have shown that genetic variation is associated with mortality
13 rates in many phenotypes of Cottonwood. Mortality rates may vary with factors such as
14 productivity and water use, which have been shown to be controlled by genetics. For
15 example, Lojewski et al. (personal communication 2006) and Oleksyn (2000) found that
16 differences in tree genotypes may lead to differences in productivity. Other studies have
17 also shown that water use may vary between *Populus* genotypes (Rowland et al. 2000).
18 Genetic variation also affects mortality in species other than cottonwood. A study
19 examining the effect of temperature selection pressure on mortality rates in *Solidago*
20 *vigaurea* (goldenrod) found significant differences in survival rates between
21 genotypes (Bjorkman 1966), and classic ecotype studies by Clausen, Keck, and Hiessey
22 (1940), found higher performance of ecotypes in environments more similar to the
23 environments of their origin. However, provenance studies in forestry frequently show

1 higher performance of higher latitude species in lower latitude climates . In the case of
2 dramatic restoration efforts along the lower Colorado river where more than 90% of an
3 environment requires direct replanting for restoration of dominant foundational species
4 (Ellison et al. 2005), increased survival of more northern genotypes at early stages of out-
5 planting could have obvious impacts.

6 This study highlights the advantages in continuous monitoring of restoration
7 sites with a diverse genetic makeup. While a site may be planted with a multitude of
8 genetically distinct individuals, overall diversity may decrease in time as a result of
9 varying degrees of fitness. Our results suggest that differences in mortality due to
10 genotype can be highly variable. Thus, caution must be placed to ensure that the final
11 genetic composition of a site is indeed the same as to that which was initially planted.

12 Our results suggest that temperature, elevation, and precipitation may all act as
13 selection pressures on genotype. Previous studies have provided evidence that genotype
14 has a propensity to determine traits and mortality relative to environmental factors. This
15 data adds to the growing body of evidence that genotypic variance between populations
16 determines fitness relative to the environmental stress of a geographic area.

17

18 **Future Study**

19 Differential survival among genotypes may lead to unexpected consequences. In
20 the three plots examined at Cibola National Wildlife Refuge, a post-planting mortality
21 rate of 31.55% was determined. Genetic variation is clearly important to the larger
22 community and ecosystem (see Whitham et al. 2006), but this same variation could also
23 result in accidental selection for genotypes from more northern environments if

1 restoration cuttings are not closely monitored. In a changing global climate, we should
2 also consider that genotypes most adapted for an altered future climate may not be the
3 most locally adapted genotypes, since local genotypes may be adapted to the current
4 climate, and not the future climate.

5 Our study looked at how genetics influence mortality. However, quantitative
6 differences between genotypes expressed in terms of genetic distance and specific traits
7 may further advance our understanding of restoration success and genetic diversity.
8 Although we can say that specific genotypes are different, we cannot easily quantify the
9 specific amount of genetic difference between genotypes. Current research is using
10 Amplified Fragment Length Polymorphisms (AFLPs; Allen and Honchack, unpublished
11 data; Whitham et al. 2006) to look to determine inter-genome differences. Using AFLP
12 data, it would be possible to measure genetic distance between genotypes from across the
13 geographic range of *P. fremontii*, and determine more precisely the amount of variance in
14 mortality explained by genetics.

15 Our study provides a foundation for these future efforts by showing that genetic
16 variation clearly matters to restoration success in *P. fremontii* forests. As such, it is likely
17 that restoration efforts often result in a genetic population significantly different from the
18 original out-plants. Selection on traits among genotypes could affect the genetic face of
19 future riparian forests along restored southwestern riparian areas.

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Figure Legends

Figure 1: Geographic dispersal of Cibola transplants

Figure 2: Variation in mean mortality rates categorized by genotype

Figure 3: Environmental variables as predictors of mortality

Table 1: AIC table ranking significance of factors in model

Table 1. Model selection criteria for selecting the best model predicting respective mortality of 16 genotypes of *P. fremontii* from across the species range planted in Cibola National Wildlife Refuge. Average climatic variables for the locations of each cutting were taken along with elevation of the homesite, and a variable reflecting the size of the initial cutting (basal stem diameter).

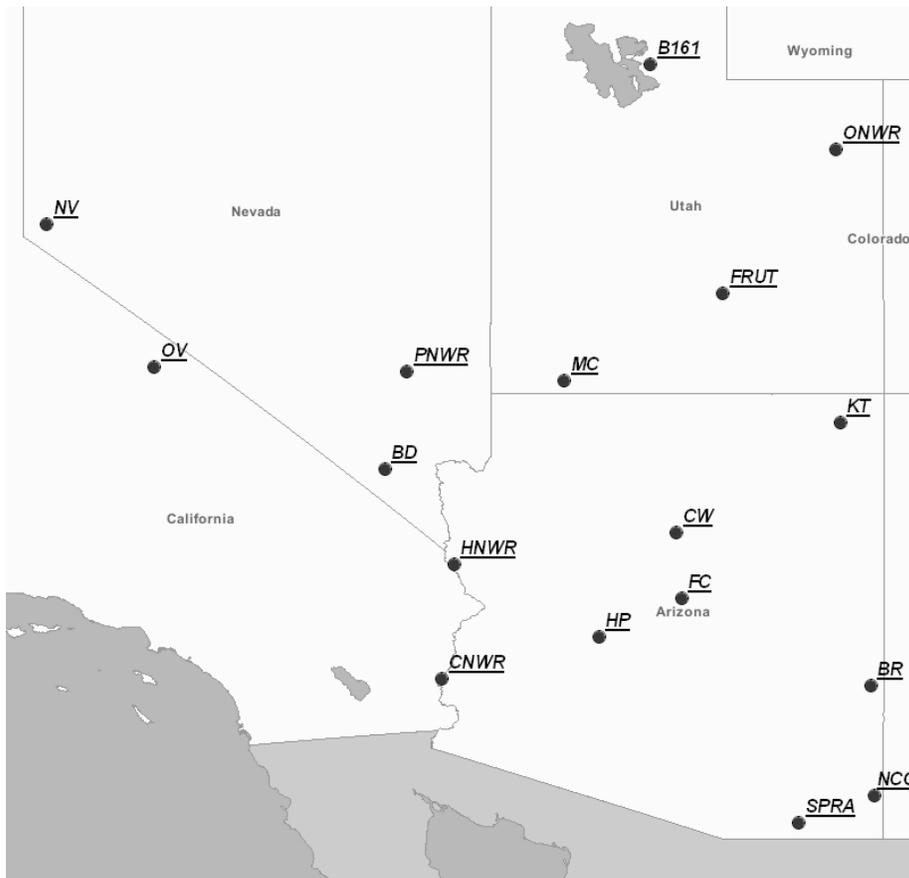
Model	AICc	DeltaAICc	Lik-Model	wi (~probabilities)	Evid. Ratio
altitude	-55.85	0 ^a	1	0.37	1
temp	-55.06	0.78 ^a	0.68	0.25	1.48
precip	-54.71	1.14 ^a	0.57	0.21	1.77
intercept	-52.13	3.72 ^b	0.16	0.06	6.41
diameter	-49.97	5.87 ^c	0.05	0.02	18.86

Note: Row titles reflect the predictive variables in the models. The “intercept” model has no predictive variables, and thus functions as a “null” model. Models are ranked from the best (top) to worst (bottom) model based on $\Delta AICc$ values (based on Akaike’s Information Criterion for small sample size (AICc)) which reflect an index of amount of information lost when approximating truth with the model. However, as a general rule, models with delta AIC_c within 2 of each other are indistinguishable in terms of fit. Letters denote statistically indistinguishable groups. Altitude is the best model for predicting mortality according to all model selection criteria, including: the $\Delta AICc$ values (lowest), the likelihood value for the best model

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1 (LIKELIHOOD; 1.0), the Akaike weight of evidence (w_i ; closest to 1), and the evidence ratio (EVID.
2 RATIO; next best model has a 1:1.5 chance of being better, given the data). This is reflected by the delta
3 AIC_c which suggests this model is statistically indistinguishable from the next three. The size of the cutting
4 (diameter) is a far worse predictor of mortality than the location the cutting came from.

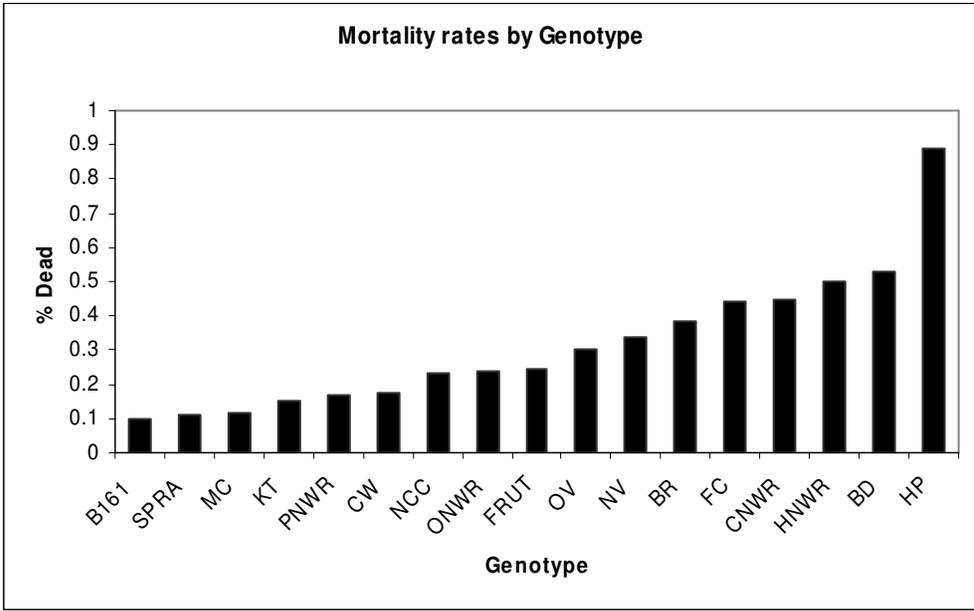
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10 Figure 1

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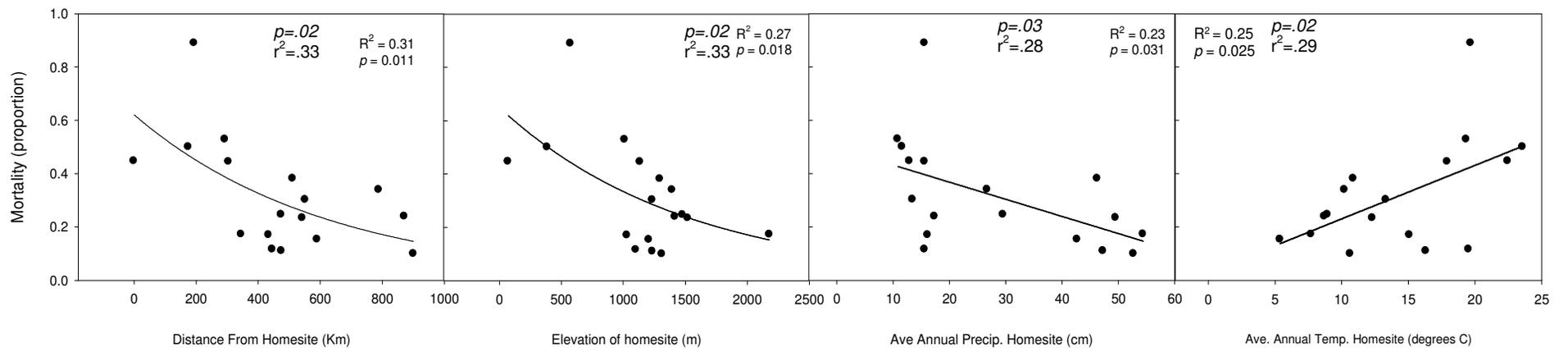


Figure 3