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The dynamics driving the invasion of *Brassica nigra* and *Foeniculum vulgare* in California : the interaction of competition, herbivory, and seed source

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Publication Date

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UNIVERSITY OF CALIFORNIA, SAN DIEGO

The dynamics driving the invasion of *Brassica nigra*
and *Foeniculum vulgare* in California:
the interaction of competition, herbivory, and seed source

A Thesis submitted in partial satisfaction of the
requirements for the degree Master of Science

in

Biology

by

Victoria Anderson Hanna

Committee in charge:

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2014

The Thesis of Victoria Anderson Hanna is approved and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2014

TABLE OF CONTENTS

Signature Page.....	iii
Table of Contents.....	iv
List of Tables.....	v
List of Figures.....	vii
Abstract of the Thesis.....	iv
Introduction.....	1
Methods.....	5
Results.....	9
Discussion.....	11
Appendix	16
Literature Cited.....	24

LIST OF TABLES

Table 1: Species used to simulate competition with a community of California native species.....	16
Table 2: Accession numbers and origins of all invasive species seeds used.....	16
Table 3: The results of a three way ANOVA examining the response of total biomass produced by <i>B. nigra</i> to three main factors.....	16
Table 4: The results of a three way ANOVA examining the response of root to shoot ratio of <i>B. nigra</i> to three main factors.....	17
Table 5: The results of a two way ANOVA examining the response of total biomass of the native community to herbivory and the different seed sources of <i>B.nigra</i>	17
Table 6: The results of a two way ANOVA examining the response of total species richness of the native community to Herbivory and different seed sources of <i>B. nigra</i>	17
Table 7: The results of a three way ANOVA examining the response of total biomass produced by <i>F. vulgare</i> to three main factors.....	18
Table 8: The results of a three way ANOVA examining the response of root to shoot ratio of <i>F. vulgare</i> to three main factors.....	18

Table 9: The results of a two way ANOVA examining the response of total biomass of the native community to herbivory and the different seed sources of <i>F. vulgare</i>	18
Table 10: The results of a two way ANOVA examining the response of total species richness of the native community to Herbivory and different seed sources of <i>F. vulgare</i>	19

LIST OF FIGURES

Figure 1: The absence of competition resulted in greater mean (\pm SD) total biomass for <i>B. nigra</i> ($p < 0.01$).....	20
Figure 2: The presence of herbivory resulted in greater mean (\pm SD) biomass for <i>B. nigra</i> ($p = 0.02$).....	20
Figure 3: <i>B. nigra</i> plants experiencing herbivory had greater mean root to shoot ratios (\pm SD) than those without herbivory ($p < 0.01$).....	21
Figure 4: The <i>B. nigra</i> population grown from seeds obtained in Italy produced greater total mean biomass (\pm SD) than those grown from seeds collected from the US or Greece locations ($p < 0.01$).....	21
Figure 5: The community of native California plants produced the greatest amount of total mean biomass (\pm SD) when grown with <i>B. nigra</i> planted from seeds collected from the California, USA location ($p < 0.01$).....	22
Figure 6: The community of native California plants, when grown with <i>B. nigra</i> , had a higher mean species richness (\pm SD) when herbivores were absent ($p = 0.05$).....	22
Figure 7: The total biomass produced by <i>F. vulgare</i> in response to competition is mediated by the presence or absence of herbivory ($p = 0.04$).....	23

Figure 8: The native community, when grown with *F. vulgare*, had a greater mean total biomass (\pm SD) when herbivory was absent (p=0.02).....

23

ABSTRACT OF THE THESIS

The dynamics driving the invasion of *Brassica nigra* and *Foeniculum vulgare* in California: the interaction of competition, herbivory, and seed source

by

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Master of Science in Biology

University of California, San Diego, 2014

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Invasive species are highly detrimental to economies and to ecosystems. To counter the negative effects of invasive plant species, a better understanding of the mechanisms driving their dominance and success is necessary. The factors of competition, herbivory, and seed source were examined using two plant species invasive to California- *Brassica nigra* and *Foeniculum vulgare*. It was found that *B. nigra* is affected by each factor individually but not by any interactions between the factors. *F. vulgare* was influenced by an interaction between competition and herbivory. Neither species appears to have evolved since its original invasive attempts.

INTRODUCTION

Invasive species cost the US an estimated \$120 billion dollars annually (Pimental, Zuniga, and Morrison 2005). Once established, invaders can severely decrease the biodiversity of the local community (Powell et al 2011, Smith et al. 2000, Lee 2002) and this loss of biodiversity can lead to highly detrimental impacts on vital ecosystem services and functions (Cardinale et al. 2012). Additionally, invasive species are a major cause of species extinction (Roberts et al 2013, Pimental, Zuniga, and Morrison 2005, Clavero and Garcia-Berthou 2006, Kappel 2005, Mack et al 2000) and, after habitat loss, are the second largest threat to biodiversity (Lake and Leishman 2004, Willis et al 2000). Invasive plant species are especially problematic because they can significantly alter native ecosystems (Mack et al 2000), and efforts to restore invaded communities are expensive, largely unsuccessful (Davies and Johnson 2011), and restricted to small spatial scales (Cione, Padget, and Allen 2002). In a review of studies where invasive plants were removed from small-scale sites, higher-level community and ecosystem characteristics did not return to pre-invasion levels and the ecological services of native communities remained permanently impaired (Corbin and D'Antonio 2011).

To counter the detrimental effects of invasive plant species on sensitive ecosystems, a better understanding of the mechanisms driving their dominance and success is necessary. Two main theories have sought to explain how exotic species can have such large impacts in areas they invade, both focused on the differential influence

of consumers in the native and invasive range of exotic species: the Evolution of Increased Competitive Ability (EICA) and the Enemy Release Hypothesis (ERH). The EICA hypothesis states that invasive species experience a release from specialist herbivores in their novel range (Blossey and Notzold 1995). Genotypes that allocate resources toward competitive ability rather than defense against specialists are selected for, resulting in the evolution of individuals with higher competitive ability compared to individuals from the native range (Blossey and Notzold 1995). For example, a recent publication by Useugi and Kessler (2013) showed that removal of above ground herbivores from groups of *Solidago altissima* for 8 years resulted in the evolution of increased competitive ability in the herbivore-excluded plants (Useugi and Kessler 2013). The increased competitive ability was only apparent in inter-specific interactions and not in intra-specific interactions, indicating that the lack of herbivory on *S. altissima* could result in this species becoming dominant in a novel range by out competing the native species for resources.

The ERH also explores the likelihood of escape from natural enemies (Keane and Crawley 2002). However, it differs from EICA in that ERH does not require that the invasive species will undergo evolution once it is released from enemies in its novel range. Instead, ERH predicts that an invasive species will respond with plasticity to allocate resources previously used for defense toward increased growth, vigor, and/or reproductive ability (Keane and Crawley 2002). An important idea that both theories share is that there must be some enemy escape or release before the species is able to reallocate resources (in the case of ERH) or to evolve (in the case of EICA).

Experiments comparing populations from the native and invasive ranges of exotic species are required to evaluate whether successful invasion is more likely attributable to a mechanism such as EICA or ERH (Oduor et al 2013, Bossdorf et al 2005, Colautti et al 2009, Siemann and Rogers 2001, Van Kleunen and Schmid 2003). For instance, a recent study used multiple seed sources in an experiment with *Brassica nigra* and found that overall, individuals grown from seeds obtained from the plant's invasive range were always taller than those grown from seeds obtained from the plant's native range (Oduor et al 2013), indicating that there had been genetic shifts in the invaded range consistent with the EICA hypothesis. Their experiments further demonstrated that the competitive ability of invaded vs. native populations was not fixed, however, because it fluctuated with the manipulation of experimental factors such as level of herbivory and plant neighbor treatment- the plasticity of a given species may only be apparent under certain experimental conditions (Oduor et al 2013). Competitive ability of invasive species is often influenced by herbivory (Agrawal et al 2012, Cano et al 2009, Coluatti et al 2009, Joshi and Vrieling 2005, Meyer et al 2005, Stastny et al 2005). However, a recent meta analysis indicates that release from herbivory alone may not be a powerful enough selective force upon invasive plant defenses (Felker-Quinn et al 2013). These findings are challenged by the study described above that found increased competitive ability in *S. altissima* after removing only the factor of herbivory (Useugi and Kessler 2013). The link between herbivory release and competitive ability likely exists, but the relative magnitude of each factor in promoting invasion remains unclear. To evaluate the relative contribution of EICA and ERH to invasion success, a field experiment was conducted focusing on two plant species invasive to California,

Foeniculum vulgare and *Brassica nigra*, a perennial and an annual species, respectively. Competition with the native plant community, the presence of herbivores, and the provenance of the invasive species seed source (native versus invasive range) were experimentally manipulated to address how these factors affect the competitive ability of these species and to test if the responses were more consistent with plasticity or evolutionary change in the invasive range. In addition, the response of the native community (biomass, species richness) were evaluated as a measure of invader impact. An interaction between the response to competition and seed source of the exotic species would indicate support for EICA, whereby growth of the focal invaders would be lowered less by competitors in the invasive range than the native range. Or, the native community would show greater suppression of growth from competition when growth with invasive populations of the exotic species compared with populations from its home range. In contrast, if ERH were contributing to invasive success, an interaction would be expected between response to herbivory and competition, such that the invasive species would be less suppressed by competition in the presence than absence of herbivores, with no difference among populations of different provenance.

METHODS

Focal invasive species

The study focused on two species invasive to California, black mustard (*Brassica nigra* (L.) Koch (Brassicaceae)) and fennel (*Foeniculum vulgare* (Apiaceae)). *B. nigra* is an annual plant native to the Mediterranean region of Europe and is considered a high level threat to local biodiversity in California (California Invasive Plant Inventory, 2006). *B. nigra* can grow over 6 feet tall and produce large amounts of small, round seeds. It possesses allelochemicals (Bell and Muller 1973) that disrupt the native plant community and may contribute to its ability to dominate in invaded regions (Turk and Tawaha 2003, Tawaha and Turk 2003). *F. vulgare* is a perennial plant native to the Mediterranean region of Europe and can form extensive monotypic stands (Ustin et al 2002) in both its invaded and native regions. *F. vulgare* can grow to be 3m tall and has a 0.9-3.0m taproot once full grown (Ogden and Rejmanek 2005). It is not known to be allelopathic.

Experimental Design

The field experiment was conducted at the University of California, San Diego Biological Field Station (32.886023, -117.230125). 30 seeds of each focal invasive species were planted in pots at the same time as the native community (30.5cm x 12.7cm x 12.7cm, Stuewe and Sons CP512) Germination varied and the invasive focal plants were thinned to obtain a maximum of five individuals per pot (all pots contained

a minimum of 3 focal plants). Pots containing each focal species were exposed to three experimentally manipulated factors in all possible combinations: competition (two levels), herbivory (two levels), and seed source (three levels), with eight replicates, resulting in a total of 192 pots.

Competition

To simulate competition within a native California plant community, a suite of seven native species were planted in half of the pots (Table 1). The rest were left without competing plants.

Herbivory

Cages were constructed (1mx1mx2m) of PVC pipe and cloth mesh to exclude all herbivores throughout the duration of the experiment. Each cage contained 16 pots in a 4x4 grid with one side accessible via velcro openings for watering access. Uncaged grids were surrounded by the cage material on 3 sides to control for cage effects such as decreased airflow and sunlight penetration while allowing herbivore access.

Seed Source

Each invasive species had three distinct seed source locations: One from the invaded (California) range and two from the native (European) range. The seeds from *B. nigra*'s European ranges came from Greece and Italy, whereas seeds from *F. vulgare*'s native European ranges were from Hungary and Italy (Appendix A, Table 2). Most seeds were acquired using the USDA GRIN database, except for the *B. nigra* seeds that came from the invaded California range, which were collected by hand in July 2013 prior to the experiment.

Biomass collection

All seeds were planted on February 27 2014, and all above and below-ground biomass was destructively harvested after three months on May 26, 2014. Each individual of the focal invasive species (*B. nigra* and *F. vulgare*), was separated with roots intact, roots were subsequently separated from shoots, keeping track of the individual identities. The remaining biomass of native species in competition pots was harvested by species, again keeping roots intact, but all biomass was pooled by species instead of at the individual level. Roots were washed free of soil over a 1 mm sieve and all samples were dried at 40°C for 48 hours. Once dry, samples were weighed to the tenth of a gram. Native species richness was based on the number of planted species that were present in the biomass at the end of the growing season.

Statistical Analyses

All analyses were done using R studio and the following packages: Companion to Applied Regression (car), Groupwise summary statistics (doBy), Scientific Graphing Functions for Factorial Designs (sciplot), Linear and Nonlinear Mixed Effects Models (nlme), and Simultaneous Inference in General Parametric Models (multcomp). I used mixed models with random effects for all tests listed below.

Three factor ANOVA tests were conducted to test for effects and interactions of the main factors (competition with native plant species, herbivory, and geographic location of the seed source) on the total biomass and root to shoot ratio of *B. nigra* and

F. vulgare. Tukey post hoc tests were conducted to determine which *B. nigra* populations were significantly different from each other in regard to total biomass produced. I calculated the mean biomass of the native community for each pot by obtaining the sum of the biomasses for each native plant growing in that pot. Two factor ANOVA tests were conducted to test for effects and interactions of caging and seed source on the total biomass and species richness of the native community when it was grown with *B. nigra* and *F. vulgare*, respectively.

RESULTS

Brassica nigra

Competition, herbivory, and seed source significantly influenced *B. nigra* biomass (Table 3). Individuals of *B. nigra* that experienced competition with native plants produced less total mean (\pm SD) biomass ($2.85\text{g} \pm 1.76\text{g}$) than individuals that did not experience competition ($4.97\text{g} \pm 2.16\text{g}$; ANOVA, $df=1$, $F=27.51$, $p<0.01$, Table 3, Figure 1). *B. nigra* plants that experienced herbivory produced more mean total biomass ($4.78\text{g} \pm 2.28\text{g}$) than those that did not experience herbivory ($3.45\text{g} \pm 2.07\text{g}$; ANOVA, $df=1$, $F=6.2$, $p = 0.02$, Table 3, Figure 2). Finally, plants grown from seeds collected in Italy had significantly higher mean biomass ($4.89\text{g} \pm 2.43\text{g}$) than those grown from seeds obtained in Greece ($3.31\text{g} \pm 1.72\text{g}$; Tukey test, $t=2.603$, $p=0.03$, Table 3, Figure 4), but not those grown from seeds obtained in the US ($3.867 \pm 2.28\text{g}$; Tukey test, $t=-1.275$, $p=0.41$). Hence, when biomass from plants grown from native range seeds (Italy and Greece together) were compared together to those grown from invaded range (California) seeds, the significant effect was no longer present ($p=0.41$). In addition, *B. nigra* individuals that did not experience herbivory had a lower root to shoot ratio (0.22 ± 0.05) than plants that experienced herbivory (0.25 ± 0.06 ; ANOVA, $df= 1$, $F =10.33$, $p<0.01$, Table 4, Figure 3).

Biomass produced by native plant species was significantly higher when grown with *B. nigra* from seeds collected in California, USA ($2.40\text{g} \pm 1.18\text{g}$) compared to

those grown with *B. nigra* from seeds collected in either European location (Italy: $1.00\text{g} \pm 0.79\text{ g}$, Greece: $1.28\text{g} \pm 0.69\text{ g}$; ANOVA, $\text{df}=2$, $F=7.58$, $p<0.01$; Table 5, Figure 5).

The native community seeded into the competition pots exhibited higher species richness when grown in the absence of herbivory vs. when grown in the presence of herbivory (2.8 ± 1.15 vs. 2.36 ± 0.93 , respectively; ANOVA, $\text{df}=1$, $F=4.06$, $p=0.05$; Table 6, Figure 6).

Foeniculum vulgare

Biomass of *F. vulgare* was influenced by an interaction between competition and herbivory (-Comp+Herb= $3.03\text{g} \pm 1.58\text{g}$, -Comp-Herb= $4.00\text{g} \pm 1.26\text{g}$, +Comp+Herb= $1.29\text{g} \pm 1.18\text{g}$, +Comp-Herb= $1.03\text{g} \pm 0.65\text{g}$; ANOVA, $\text{df}=1$, $F=4.55$, $p=0.04$; Table 7, Figure 7). The sum of squares in the ANOVA results (Table 7) shows that the interaction effect accounted for 5.61 % of the variability, whereas competition accounted for the largest amount of variability (86.4%) and herbivory accounted for only 1.6% of the variability. When herbivory was not present, there was higher species richness in the native community planted in competition with *F. vulgare* (2.95 ± 0.83 vs 2.13 ± 0.96 , ANOVA, $\text{df}=1$, $F=6.6$, $p=0.02$; Figure 8).

DISCUSSION

B. nigra

B. nigra produced less biomass when it experienced competition with the native plant community. This is perhaps unsurprising, as growth of exotic species is often suppressed by competition with native species (Lonsdale and Farrell 1998, Willis et al 1998, Muller-Scharer 1991). Interestingly, *B. nigra* had higher growth in the presence of herbivory, suggesting a trade-off between allocation to competition versus defense. When grown without herbivores, *B. nigra* may compete so intensely for resources that this intraspecific competitive pressure lessens the overall biomass produced by the population. When herbivores are present, they may cause a reallocation of resources from growth to defense and lessen the intraspecific competitive pressure enough that the overall biomass increases. A potential mechanism for this is the allocation of resources to root biomass; when herbivory is present, the plants produce more root biomass compared to when herbivores are absent. The presence of herbivores may influence the increased investment into root biomass, allowing *B. nigra* to access more resources and therefore increase in overall biomass. This result is likely due to overcompensation, which is when plants have higher fitness after herbivory than without herbivory (Poveda et al 2012) and has been observed in multiple studies (Olejniczak 2011, Paige and Whitham 1987, Lowenberg 1994, Lennartsson et al 1997, Agrawal et al 1999, Tuomi et al 1994).

The tested outcomes for native range plants were not significantly different in comparison to those from the invaded range plants. This indicates that the competitive ability that *B. nigra* possesses is likely due to plasticity and not due to the evolution of increased competitive ability. However, the native community performed better when grown with *B. nigra* from the US location in comparison to either of the EU locations. This indicates that the US location does not have as high of a competitive ability as the EU populations. This could be due to the EU populations being better competitors, or it could be that the native community has coevolved to compete well with the US populations of *B. nigra*. It is likely that the EU populations are better competitors than those from the US; plants grown from seeds from Italy outcompeted those grown from seeds from Greece or the US. This result supports the theory behind Enemy Release Hypothesis (Keane and Crawley 2002) over the theory of the Evolution of Increased Competitive Ability (Blossey and Notzold 1995). If *B. nigra* were behaving under the assumptions of EICA, the US populations would have outperformed the EU populations. To further verify these findings, collection of multiple populations of *B. nigra* from CA and EU for experimental use is needed.

Herbivory lowered species richness in the native community, likely due to selective removal of palatable species (Caswell et al 1973).

Foeniculum vulgare

The total biomass (proxy for competitive ability) of *F. vulgare* was affected by the interaction of competition and herbivory. The response of *F. vulgare* to competition

was mediated by the presence or absence of herbivory: when herbivores were present, the reaction to competition was less intense compared to when herbivores were absent. The factors of herbivory and competition have generally negative effects on plant performance (Hambäck and Beckerman 2003, Haag et al 2004, Schädler et al 2007). While a recent study confirmed the interaction of these two factors in an invasive species (Huang et al 2012), the literature is lacking when it comes to the examination of the interaction of these traits in invasive species. Further research in this area will likely result in better methods for managing invasive plant populations.

In contradiction to the prediction of EICA, the seed source of *F. vulgare* did not have a significant effect on its competitive ability as both total biomass and root to shoot ratio were unaffected. Because populations of *F. vulgare* grown from native or invaded seed sources performed similarly under the same conditions, the initial establishment of this species in the CA ecosystem is likely influenced by the factors explained in ERH. That is, this species is likely plastic with regard to its competitive ability and invasive potential in this ecosystem. This provides further support for ERH, which has already been supported in much of the literature (See Liu and Stiling 2006, Vila et al 2005, Adams et al 2009, Genton et al 2005, Agrawal et al 2005, Andonian et al 2012). The biomass of the native community was not significantly affected by seed source of *F. vulgare* or the manipulation of herbivory.

The diversity of the native community was not affected by the seed source of *F. vulgare*, indicating that the populations can be considered relatively equal with regard

to competitive ability. However, the diversity of the native community was influenced by herbivory: when herbivory was not present, the community had higher species richness. A similar result was seen when the native community was grown with *B. nigra*; this is directly in contrast with the Janzen-Connell hypothesis, but this may result may be due to the short time period of the experiment (see Allan and Crawley 2011) .

Many studies argue for EICA being predominant successful strategy for invasive species (Blossey and Notzold 1995, Uesegi and Kessler 2013, Agrawal et al 2012, Colautti et al 2009, Feng et al 2009, Franks et al 2008, Bossdorf et al 2005, Joshi and Vrieling 2005, Siemann and Rogers 2001, Willis et al 1999), yet several studies contradict this idea in favor of ERH (Felker-Quinn et al 2013, Cano et al 2009, Colautti et al 2009, Cripps et al 2008, Franks et al 2008, Hull Sanders et al 2007, Van Kleunen and Schmid 2003). This debate about which theory most supports successful invasions may be alleviated if a connection between invasive potential and life history is found.

This study illustrates the importance of having diverse data on factors that may contribute to the competitive ability of a species. Many studies attempt to elucidate the competitive ability of a plant by examining plant growth (Vila et al 2005, Bossdorf et al 2005, Coluatti et al 2009, Siemann and Rogers 2001, Van Kleunen and Schmid 2003, Meyer, Clare, and Weber 2005, Cripps et al 2008 Stastny et al 2005) or reproductive traits (Coluatti et al 2009, Agrawal et al 2012, Van Kleunen and Schmid 2003, Meyer, Clare, and Weber 2005, Stastny et al 2005). While these methods are generally good indicators of a plant's competitive ability, this study illustrates the need to examine the

response of the competitors. Through the analysis of the community of natives, it was discovered that there was a difference in the competitive ability of different *B. nigra* populations. If the response of the native community was not examined, this result would have been missed entirely. Future studies that attempt to quantify the competitive ability of a plant would be well advised to examine the individual or community that their target plant is competing with.

APPENDIX

Tables

Table 1: Species used to simulate competition with a community of California native species.

Species name	Common name
<i>Amsinckia tessellata</i>	Bristly fiddleneck
<i>Escholzia californica</i>	California poppy
<i>Festuca rubra</i>	Red fescue
<i>Hemizonia fasciculata</i>	Clustered tarweed
<i>Lasthenia californica</i>	California goldfields
<i>Nassella pulchra</i>	Purple Needlegrass
<i>Sisyrinchium bellum</i>	Californian blue-eyed grass

Table 2: Accession numbers and origins of all invasive species seeds used.

Species and location	Accession Number (USDA GRIN)	Origin
<i>Brassica nigra</i>		
Location 1	NA; collected for this study	San Diego, California
Location 2	PI 633147	Greece
Location 3	PI 633148	Italy
<i>Foeniculum vulgare</i>		
Location 1	NSL 6409	California
Location 2	PI 531336	Hungary
Location 3	Ames 27588	Italy

Table 3: The results of a three way ANOVA examining the response of total biomass produced by *B. nigra* to three main factors: competition (Comp), herbivory (Herb), and seed source (source). An * indicates a significant effect.

Factor	Sum of Squares	Degrees of freedom	F value	P value
Comp	95.31	1	27.51	<0.01*
Herb	21.49	1	6.20	0.02*
Source	38.88	2	5.61	<0.01*
Comp x Herb	4.74	1	1.37	0.25
Comp x Source	3.89	2	0.56	0.57
Herb x Source	2.67	2	0.39	0.68
Comp x Herb x Source	1.41	2	0.20	0.82
Residuals	252.89	73		

Table 4: The results of a three way ANOVA examining the response of root to shoot ratio of *B. nigra* to three main factors: competition (Comp), herbivory (Herb), and seed source (Source). An * indicates a significant effect.

Factor	Degrees of freedom	F value	P value
Comp	1	0.05	0.82
Herb	1	10.33	<0.01*
Source	2	0.94	0.39
Comp x Herb	1	0.17	0.68
Comp x Source	2	0.23	0.80
Herb x Source	2	1.56	0.22
Comp x Herb x Source	2	0.36	0.70

Table 5: The results of a two way ANOVA examining the response of total biomass of the native community to herbivory (Herb) and the different seed sources of *B.nigra* (Source). An * indicates a significant effect.

Factor	Degrees of freedom	F value	P value
Herb	1	2.24	0.14
Source	2	7.58	<0.01*
Herb x Source	2	0.94	0.40

Table 6: The results of a two way ANOVA examining the response of total species richness of the native community to Herbivory (Herb) and different seed sources of *B. nigra* (Source). An * indicates a significant effect.

Factor	Degrees of freedom	F value	P value
Herb	1	4.06	0.05*
Source	2	0.48	0.63
Herb x Source	2	0.23	0.80

Table 7: The results of a three way ANOVA examining the response of total biomass produced by *F. vulgare* to three main factors: competition (Comp), herbivory (Herb), and seed source (Source).

Factor	Sum of Squares	Degrees of freedom	F value	P value
Comp	105.08	1	70.52	<0.01*
Herb	1.94	1	1.30	0.26
Source	1.03	2	0.35	0.71
Comp x Herb	6.78	1	4.55	0.04*
Comp x Source	0.91	2	0.30	0.74
Cage x Source	1.52	2	0.51	0.60
Comp x Herb x Source	3.64	2	1.22	0.30
Residuals	89.40	60		

Table 8: The results of a three way ANOVA examining the response of root to shoot ratio of *F. vulgare* to three main factors: competition (Comp), herbivory (Herb), and seed source (Source).

Factor	Degrees of freedom	F value	P value
Comp	1	1.90	0.17
Herb	1	3.02	0.09
Source	2	0.91	0.41
Comp x Herb	1	0.10	0.75
Comp x Source	2	0.85	0.43
Herb x Source	2	0.47	0.63
Comp x Herb x Source	2	2.17	0.12

Table 9: The results of a two way ANOVA examining the response of total biomass of the native community to herbivory (Herb) and the different seed sources of *F. vulgare* (Source).

Factor	Degrees of freedom	F value	P value
Herb	1	0.45	0.51
Source	2	0.70	0.51
Herb x Source	2	0.19	0.83

Table 10: The results of a two way ANOVA examining the response of total species richness of the native community to Herbivory (Herb) and different seed sources of *F. vulgare* (Source).

Factor	Degrees of freedom	F value	P value
Herb	1	6.60	0.02*
Source	2	1.50	0.24
Herb x Source	2	0.05	0.95

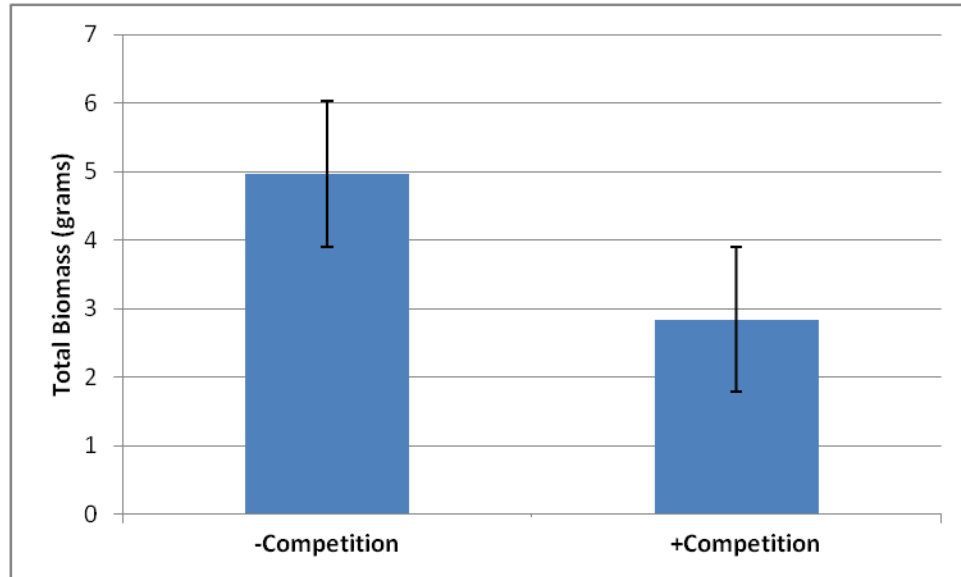
Figures

Figure 1: The absence of competition resulted in greater mean (\pm SD) total biomass for *B. nigra* ($p < 0.01$).

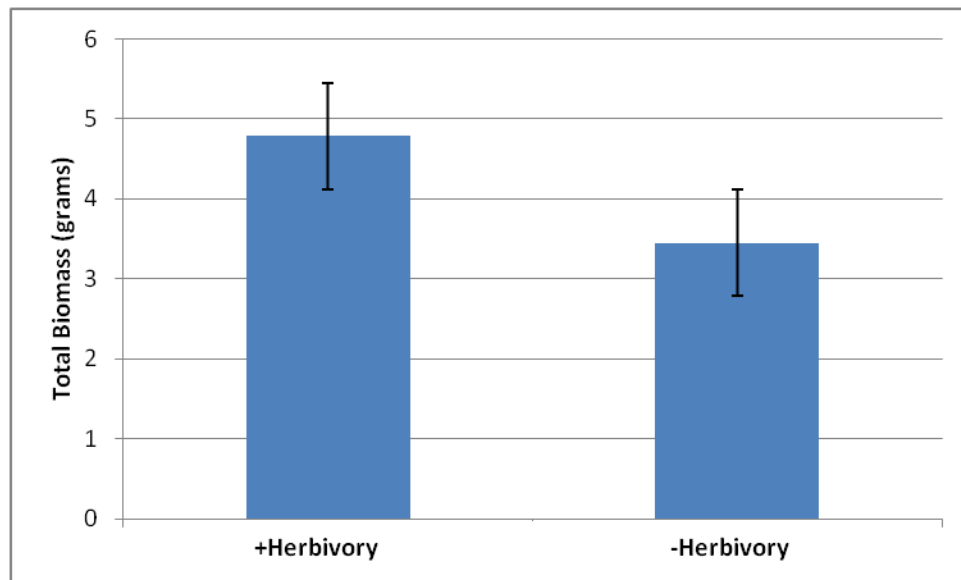


Figure 2: The presence of herbivory resulted in greater mean (\pm SD) biomass for *B. nigra* ($p = 0.02$).

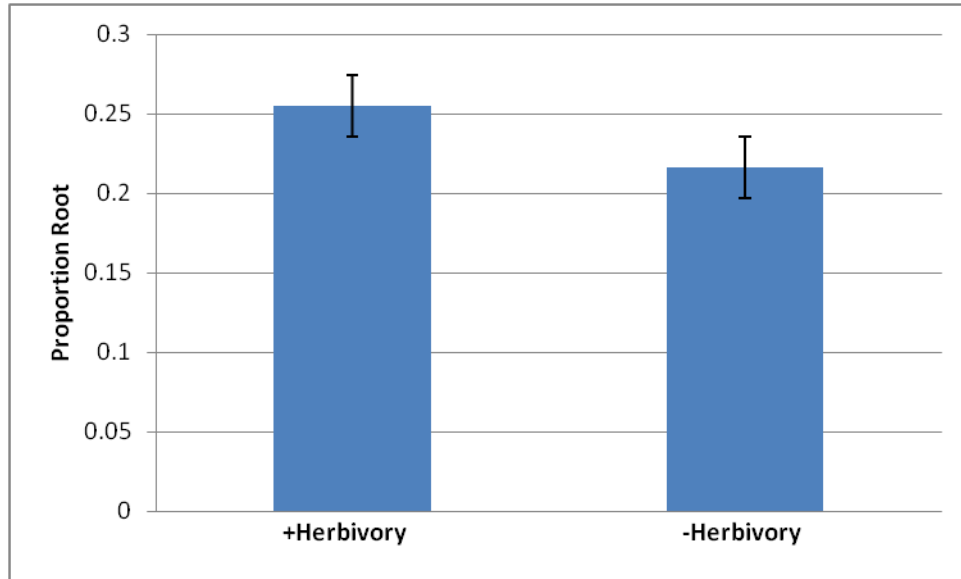


Figure 3: *B. nigra* plants experiencing herbivory had greater mean root to shoot ratios (\pm SD) than those without herbivory ($p < 0.01$).

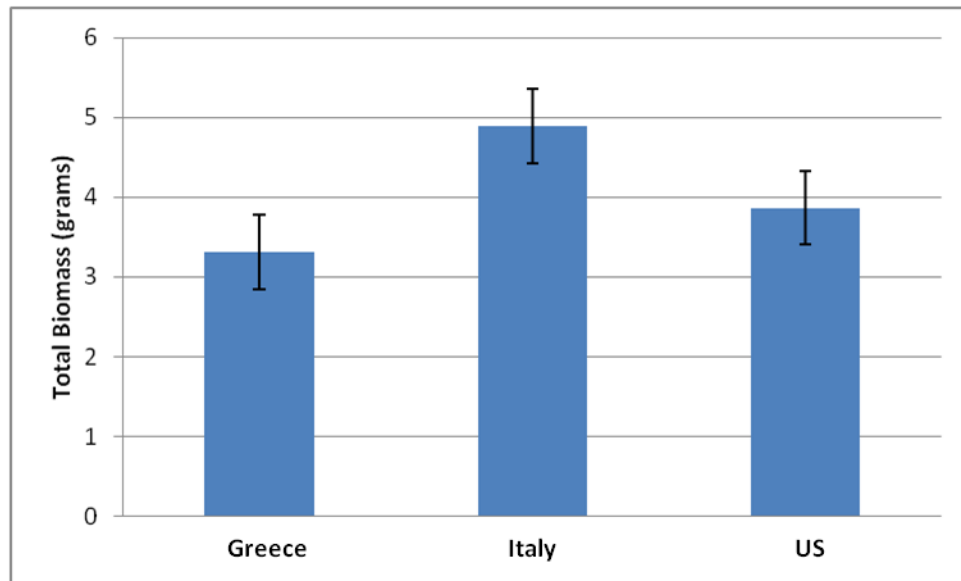


Figure 4: The *B. nigra* population grown from seeds obtained in Italy produced greater total mean biomass (\pm SD) than those grown from seeds collected from the US or Greece locations ($p < 0.01$).

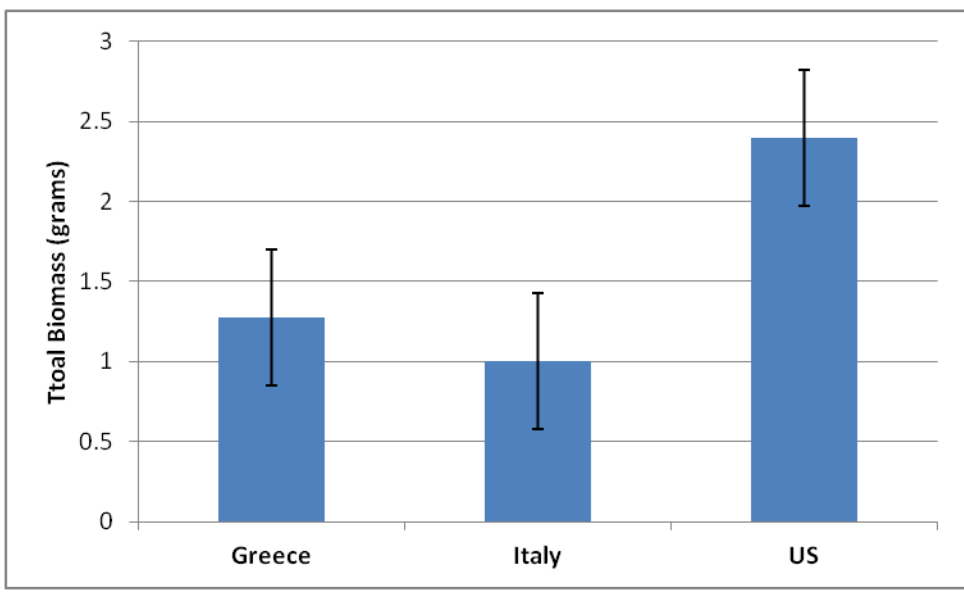


Figure 5: The community of native California plants produced the greatest amount of total mean biomass (\pm SD) when grown with *B. nigra* planted from seeds collected from the California, USA location ($p < 0.01$).

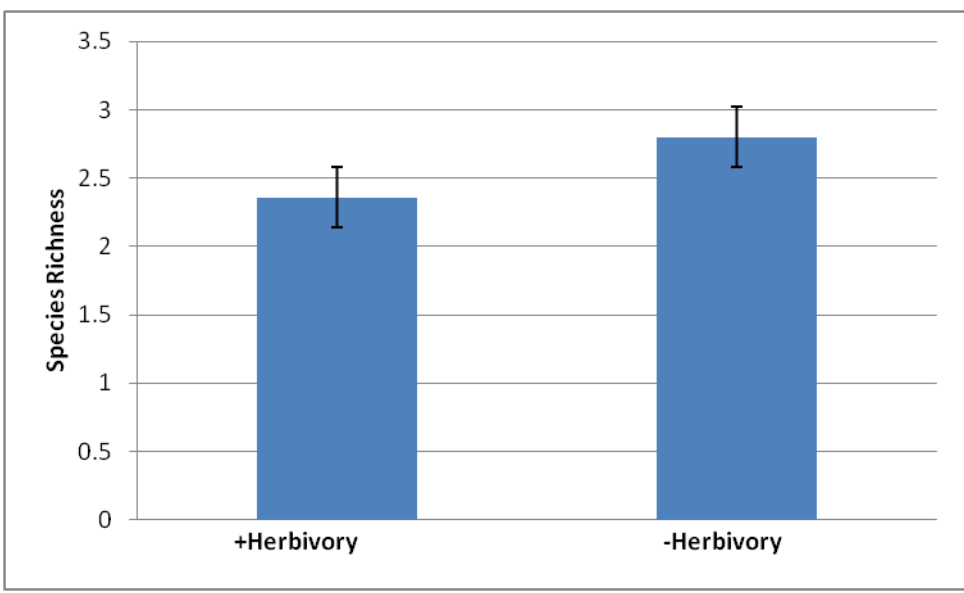


Figure 6: The community of native California plants, when grown with *B. nigra*, had a higher mean species richness (\pm SD) when herbivores were absent ($p = 0.05$).

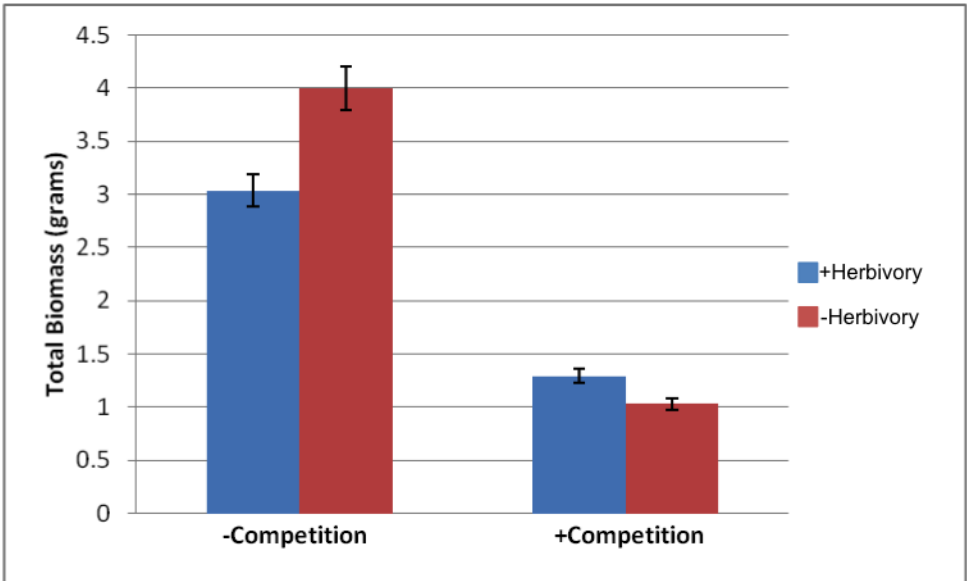


Figure 7: The total biomass produced by *F. vulgare* in response to competition is mediated by the presence or absence of herbivory ($p=0.04$). When herbivory is present, the reaction to competition is less intense in comparison to when herbivory is absent.

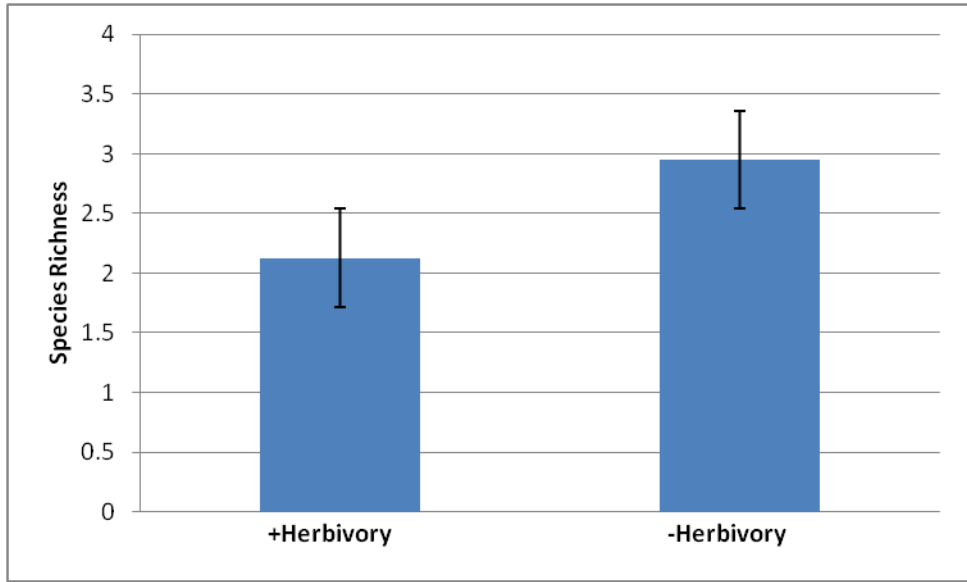


Figure 8: The native community, when grown with *F. vulgare*, had a greater mean total biomass (\pm SD) when herbivory was absent ($p=0.02$).

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