Differential Phenology of Invasive Mustards and the Natives at Risk: How does Sahara Mustard Succeed in Southwestern Deserts?

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Abstract

Sahara mustard (*Brassica tournefortii)* is an exotic species that has recently expanded throughout southwestern US deserts, while related exotic species with partially overlapping ranges (black mustard, *Brassica nigra*, and shortpod mustard, *Hirschfeldia incana* [formerly *Brassica geniculata*]), have not invaded desert areas. We compared these three mustard species and desert and non-desert populations of Sahara mustard to determine possible mechanisms for differential invasion patterns. In germination experiments, interactions were found between plant type (species or population) and temperature and moisture treatments, but days to first emergence and total germinability did not differ and all types were affected similarly by low soil moisture. Furthermore, desert populations of Sahara mustard did not have faster or higher percentages of germination at high temperatures, and germination of black mustard, the most coastal type, was not inhibited by high temperature. These results indicate that expansion of Sahara mustard in the desert is not due solely to seed characteristics. In pot experiments, desert and non-desert populations of Sahara mustard behaved similarly, while both populations bolted and flowered sooner than the other two species. In desert field plots, Sahara mustard emerged, bolted, flowered, and set seed earlier than native annual species at the same site. Our results suggest that local adaptation to the desert environment has not occurred in Sahara mustard, rather that phenological differences between species allow Sahara mustard to complete its life cycle early in winter and avoid harsh conditions. Contrary to expectations, native annuals grew larger and set seed earlier in plots containing Sahara mustard, indicating that site suitability for plant growth might be more important than competition in regulating distribution of native and exotic species. These results suggest that areas of greatest conservation value are likely most vulnerable to Sahara mustard invasion, particularly in wet years when seeds are not moisture limited.

Introduction

Brassica tournefortii (Sahara mustard) is an exotic annual mustard currently spreading in southwestern deserts, including the Mojave. *B. tournefortii*, or Sahara mustard, is one of only a few exotic plants able to spread rapidly and dominate desert ecosystems. It first appeared in the Coachella Valley in 1927 (Sanders and Minnich 2000), and has since has spread via roadsides, vehicles, wind and wildlife, especially in years of high precipitation. However, it was not until recently that *B. tournefortii* was widely recognized as an ecological threat to native desert ecosystems (Desert Managers Group 2005). The recent, rapid expansion and widespread dominance of *B. tournefortii* in previously uninhabited areas suggests that the species may have experienced a recent adaptation to extremely arid environments that allowed its expansion (e.g Aronson et. al. 1992), or experienced a "lag time" in its invasion process, establishing small populations for many years before exploding into large, dominant populations during high precipitation seasons.

Unlike other related invasive mustards such as *B. nigra* and *Hirschfeldia incana*, *B. tournefortii* has not yet been studied as an invasive species, and almost nothing is known about its phenology, seed ecology, or effects on native plant species. Furthermore, *B. tournefortii* is so far the only exotic mustard to spread successfully into the Mojave and other extreme desert ecosystems, providing a unique opportunity to determine characteristics that may enable exotic plants to successfully invade desert ecosystems.

The purpose of this study was 1) to characterize phenology of *B. tournefortii* in desert ecosystems and 2) to investigate phenological differences between populations from desert ecosystems and less stressful environmentsas a possible mechanism of invasion. The research focused on the phenology of both seeds and plants of *B. tournefortii* ecotypes in comparison to other exotic mustard species, and also compared the phenology of *B. tournefortii* in the Mojave with that of native desert annuals.

Methods and Materials

Seed Biology:

- Seeds from two *Brassica tournefortii* (Riverside and Coachella Valley), one *B. nigra* (Crystal Cove) and one *Hirschfeldia incana* (Riverside) populations were used in this study. Each population was considered a "biotype" representing potential groups of adaptive responses. Seeds were randomly mixed from several plants in each population.
- A split-split plot with randomized complete block design was used with three replications. The main plots represented the three temperature regimes (Riverside at 22.6/9 oC, El-Centro at 27/10.3 oC and Davis at 19/6.6 oC), the subplots consisted of the four biotypes, and the sub-subplots included the three water potential treatments (0, -1 and –5).
- Under each treatment, 50 seeds of each biotype were planted in five 5-cm pots. Pots were weighed every other day and water was added to maintain the desired water potentials. Germinated seeds were recorded and removed over a period of four weeks and percent germination was calculated.
- Three trials (reps.) were run on July15, 2004, November11, 2004 and April 8, 2005. Three germinator chambers were used, and temperatures were switched in repeated experiments so that each chamber was used for each temperature regime to minimize pseudoreplication.
- Data was log- transformed for analysis and back-transformed for presentation. Analysis of variance and LSD tests were performed using Statistix 8.0.

Exotic Mustard Phenology:

- Two common garden experiments; one at UC Riverside, Riverside CA, one in Blue Diamond, near Las Vegas NV.
- Split plot randomized complete block design testing phenology of same 4 "biotypes" tested in seed biology study, 2 populations per "biotype." 8 populations * 8 blocks (reps.) = 64 pots/location.
- 8 seeds were germinated in 9.6 L pots outdoors at each location beginning Dec. 23 and 24. Seedlings were thinned to 2 per pot when true leaves developed and kept amply watered throughout the life cycle. Plants were fertilized for 1 month beginning 3/4/05 in Riverside due to nutrient leaching by heavy rains. Plants were harvested at seed dispersal: late June in Las Vegas, late July in Riverside. From thinning, the height, 2 widths, cotyledon presence/absence, leaf number, and phenologic stage were recorded weekly.
- Temperatures recorded onsite by single-channel HOBO sensors (Figure 1).
- Data analyzed using Kolmogorov-Smirnov tests between populations of the same biotypes both within and between locations, and between the same biotypes at different locations.

Native and B. tournefortii *Phenology in the Mojave*:

- Field site: Between Barstow and Baker cities along Interstate 15 at Rasor Rd., near dry Cronese Lakes. Site characterized by creosote scrub in sandy soils.
- *B. tournefortii* distributed along a gradient of high density near Rasor Rd. decreasing with distance from the road, but patchy throughout. 6 transects 30 m long laid parallel to road with distances of 30 – 50 m in between transects. Plots measuring .5 x 1 m laid at 3 m intervals along each transect for a total of 60 plots.
    - *Diversity and Dominance*: Total counts and category cover estimates of each plant species were recorded in all 60 plots monthly from Jan. – Apr., 2005.
    - *Phenology and Growth*: 20 plots were chosen for subsampling of individual plant species by grouping the *B. tournefortii* densities into 5 groups ranging from 0 to 60 plants per plot. Total plant density within each plot was kept relatively even. About 10 plants of *B. tournefortii* and 3 chosen native species were individually labeled in each of the 20 plots. The 3 native species chosen were *Camissonia claviformis, Chaenactis stevioides,* and *Cryptantha angustifolia*. Height, 2 widths, and life stage were recorded for each labeled plant bimonthly from late Jan. to April, 2005.
- Data analyzed using linear regression to compare the correlation of *B. tournefortii* density with growth and phenology of natives.

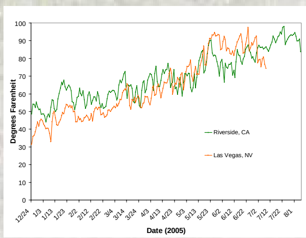

Figure 1: Temperature (° F) for each common garden experiment during study.

Individually labeled seedlings of *B. tournefortii* and native plants in a .5 x 1 m plot at Rasor Rd. field site, Mojave Desert.

Results: *Seed Biology*

- Biotypes did not differ in total germination over all treatments, but interactions were significant (Table 1).
- Temperature and water potential affected all biotypes differently both alone and in combination (Table 1).
- Desert (CV) *B. tournefortii* did not have greater germination than any other biotype at any temperature and/or water combination. (Figure 2a,b,c)
- Although *B. nigra* is the most coastal biotype, high temperature did not inhibit germination compared with other biotypes. (Figure 2c).
- Germination was slower in *B. nigra* than in the other three biotypes (Table 2).
- Low water potentials slowed germination in all four biotypes (Table 3).
- Biotypes did not differ in germination rate with temperature (Table 4).

Table 1: Effects of temperature, water potential and biotype on germination of the four tested biotypes under three water potential treatments and three temperature regimes.

Source of Variation	DF	SS	MS	F
Replication (Rep)	2	0.29182	0.14591	
Temperature (Temp)	2	0.07846	0.03923	0.35
E_a	4	0.45235	0.11309	
Biotype (Bio)	3	0.09001	0.03	0.68
Temp*Bio	6	1.1578	0.19297	4.38*
E_b	18	0.7932	0.04407	
Water Potential (WP)	2	2.25783	1.12891	61.94**
Temp*WP	4	0.2346	0.05865	3.22*
Bio*WP	6	0.34006	0.05668	3.11*
Temp*Bio*WP	12	0.75312	0.06276	3.44*
E_c	48	0.87482	0.01823	
Total	107	7.32407		

*, ** significant at 0.05 and 0.01 probability level, respectively

Table 2: Mean days to germination* in 4 Brassica biotypes under 3 temperature regimes and 3 water potential treatments.

Biotype	Days to Germination
BN-CC	5[a**]
BT-UC	3.5[b]
BG-Riv	3.4[b]
BT-CV	3.3[b]

* Data was back-transformed for presentation.
** Means followed by the same letter are not significantly different at the 5% probability level.

Table 3: Mean days to germination* under 3 water potential treatments.

Water Potential	Days to Germination
Zero	3.1[a**]
Minus One	3.4[a]
Minus Five	5[b]

* Data was back-transformed for presentation.
** Means followed by the same letter are not significantly different at the 5% probability level.

Table 4: Mean days to germination* under 3 temperature regimes

Temperature	Days to Germination
Davis	4.4
El-Centro	4
Riverside	3.7

* Data was back-transformed for presentation.

NB: No significant interactions were found between any two of the three factors: temperature, biotype and water potential.

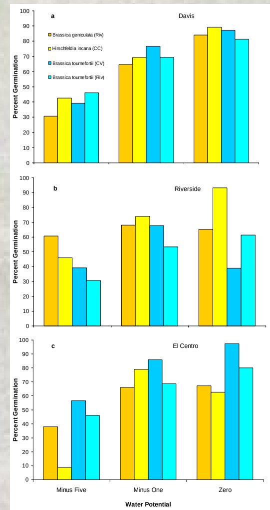

Figure 2: a) Percent germination in 4 *Brassica* biotypes under 3 water potential treatments, 19/6.6 °C (Davis). b) Percent germination in 4 *Brassica* biotypes under 3 water potential treatments, 22.6/9 °C (Riverside). c) Percent germination in 4 *Brassica* biotypes under 3 water potential treatments, 27/10.3 °C (El Centro).

Conclusions

- Although germination in *H. incana* and *B. nigra* does not appear to be more limited by temperature or water stress than in *B. tournefortii*, *B. tournefortii* develops more rapidly. *B. tournefortii's* phenology may allow it to reproduce in time to escape drought stress, succeeding in fitness where the other species may fail (Grime 1977). This may account for *B. tournefortii's* ability to invade desert ecosystems.
- There is no evidence from this study that *B. tournefortii* has invaded the Mojave desert due to local adaptation.
- Site characteristics may be important for both *B. tournefortii* and native plant success. The positive correlation between native plant size and cover and *B. tournefortii* density and cover indicates that *B. tournefortii* may be preferentially invading sites that are most beneficial for some native plants and diminishing native plant density.
- This observation is important to land management because it indicates that sensitive areas of greatest value to conservation may be most vulnerable to invasion.

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Results: *Exotic Mustard Phenology*

- *B. tournefortii* had a faster rate of development than *B. nigra* and *H. incana*, respectively, in both Las Vegas and Riverside locations (Figure 3a, b. Figure 4a, b).
- There was no difference between *B. tournefortii* "Desert" and "Inland" populations either within the two locations or between locations.

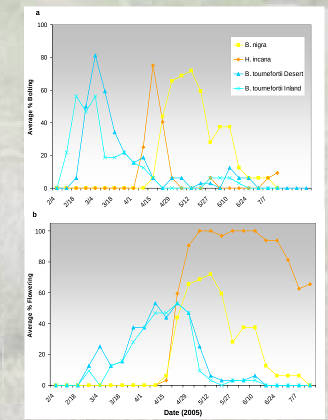

Figure 3: a) Percent (%) bolting by date and biotype in Riverside, CA. b) Percent (%) flowering by date and biotype in Riverside, CA.

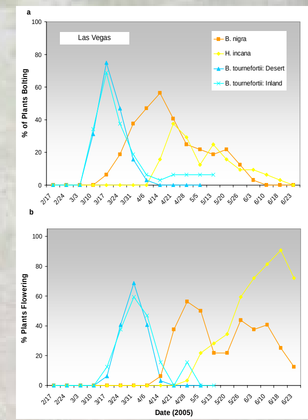

Figure 4: a) Percent (%) bolting by date and biotype in Las Vegas, NV. b) Percent (%) flowering by date and biotype in Las Vegas, NV.

Results: *Native and* B. tournefortii *Phenology in the Mojave*

- *B. tournefortii* exhibits a pattern of early and rapid development in the Mojave Desert environment (Figure 5a).
- *B. tournefortii* developed faster than either *Chaenactis stevioides* or *Cryptantha angustifolia* (Figures 5b, c).
- Native plant diversity was unaffected by *B. tournefortii*, but native plant density decreased with increasing B. tournefortii cover. Native plant cover increased with increasing *B. tournefortii* cover (Table 5).
- *Chaenactis stevioides* and *Cryptantha angustifolia* tended to be larger with higher *B. tournefortii* density and/or cover, and *Chaenactis* bolted earlier with high *B. tournefortii* density (Table 5).

Table 5: Correlations of *B. tournefortii* and native plants to *B. tournefortii* density and cover.

	B. tournefortii January Density	January Cover	February Density	February Cover	March Density	March Cover
Native Diversity	NS*	NS	NS	NS	NS	NS
Native Density	NS	↓ ** 0.0496	NS	↓ 0.0494***	NS	NS
Native Cover	NS	0.0246	NS	NS	NS	NS
B. tournefortii						
Growth (Height)	NS	NS	↑ 0.001	NS	NS	NS
Bolting Date	NS	NS	NS	NS	NS	NS
Flowering Date	↑ 0.0036	↑ 0.0151	NS	↑ 0.0242	NS	NS
Seed Set date (& %)	↑ 0.0005	NS	↑ 0.0042	NS	↑ 0.0041	NS
Chaenactis stevioides						
Growth (Height)	NS	NS	↑ 0.035	NS	↑ 0.0383	NS
Bolting Date	NS	NS	↑ 0.0382	NS	↑ 0.0125	NS
Flowering Date	NS	NS	NS	NS	NS	NS
Seed Set Date	NS	NS	NS	NS	NS	NS
Cryptantha angustifolia						
Growth (Height)	NS	NS	↑ 0.0034	↑ 0.0014	↑ 0.0116	NS
Bolting Date	NS	NS	NS	NS	NS	NS
Flowering Date	NS	NS	NS	NS	NS	NS
Seed Set Date	NS	NS	NS	NS	NS	NS

*NS = Not Significant
** Arrows indicate increase or decrease response of row variable to column factor.
*** Data are P values significant at 5% level

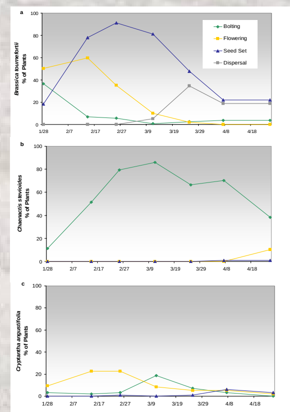

Figure 5: a) Phenology of *B. tournefortii* in the Mojave Desert. b) Phenology of *Chaenactis stevioides* in the Mojave. c) Phenology of *Cryptantha angustifolia* in the Mojave.

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