Recruitment Failure of Chenopod Shrub Populations in the Great Basin

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Abstract: The salt desert shrub ecosystem has suffered increasing invasion by exotic annual weeds, especially cheatgrass, for the last 25 years or longer. After the extensive shrub dieoffs of 1982 to 1984 in the Great Basin and Colorado Plateau, many shadscale (*Atriplex confertifolia*) and winterfat (*Ceratoides lanata*) populations failed to regenerate. Several facultatively pathogenic fungi were isolated from the rhizosphere of shadscale. Levels of soil *Fusarium* and pythiaceous fungi in intact and dieoff shrubland areas were measured with positive correlation between fungal density and dieoff severity of shadscale in one study and winterfat in a separate study. Shadscale seedings in three shadscale sites invaded by annual weeds in the Utah western desert resulted in significant seedling emergence followed by 100 percent establishment failure. Seedlings with wilt symptoms were observed in each of these studies. In each case soil moisture was adequate for seedling establishment. A greenhouse test was conducted to study seedling establishment of these two species in 10 valley bottom soils, four from recruiting shrub populations and six from defunct shrub sites invaded by cheatgrass or halogeton. Autoclaved and fungicide-treated soil treatments significantly increased winterfat seedling survival ($P > 0.001$) in soils from weed-invaded sites. No effect of soil treatment was seen in shadscale seedling numbers in this study. Winterfat seedling weight was not affected by soil treatment and did not differ between soil sites. Shadscale seedling weight was significantly increased by soil treatment in intact soils but not in weedy soils. In a separate emergence study shadscale fruits were planted in soil from two intact and two weed-invaded shadscale sites. After moist chilling at 2 °C, more than twice as many live seedlings were observed in the two soils from intact sites as in the two soils from weed-invaded sites. Work in progress will attempt to isolate a causal organism from dying shadscale seedlings. Shadscale sensitivity to fungicides will also be investigated.

Introduction

The salt desert shrub ecosystem in Western North America is second in area only to the sagebrush ecosystem. It covers over 17 million ha of lowlands, with the dominant perennial plants being shrubs from the chenopod family (West 1994). During the last 25 to 50 years increasing invasion of alien grasses and other annual plants has led to recurring fires and expanding invasion of weeds; in many cases the native shrub communities have not returned.

An extensive shrub dieoff occurred in the Great Basin and Colorado Plateau in the early 1980s, coinciding with a series of "El Niño" years that resulted in record high precipitation. This dieoff affected chenopod shrubs, particularly shadscale (*Atriplex confertifolia*) in most Great Basin valleys. The Bureau of Land Management (BLM) estimated that more than 280,000 ha of shadscale were lost in Utah alone (Nelson and others 1989). This dieoff was followed by a massive invasion of annual weeds and a subsequent series of wildfires. Shadscale recruitment in most burned dieoff areas was, and remains, almost nonexistent. It is common for shadscale populations to experience cyclic dieoff and recruitment events, made possible by a long-lived soil seed bank (Sharp and others 1990), but the recruitment phase of that cycle has failed to occur in many populations, and shadscale seed banks may have become depleted. Widespread decline and recruitment failure of winterfat (*Ceratoides lanata*), a shrub second only to shadscale in abundance in salt desert shrubland, has also occurred in many Great Basin valleys (Kitchen 2001; Nelson and others 1989). Thus substantial decreases of two major shrubs have resulted in large acreages of valley bottoms susceptible to invasion by cheatgrass (*Bromus tectorum*), halogeton (*Halogeton glomeratus*), and other weeds.

Previous Research

This paper will review published studies explaining the causes of this phenomenon and describe more recent preliminary studies carried out in our laboratory. Studies carried out during and shortly after the 1980s El Niño investigated, among other factors, the role of pathogenic fungi in the dieoff. Shadscale roots were exhumed, and fungal isolations were made from surface-sterilized tap and secondary roots, as well as crowns and stems (Nelson and others 1990). Hundreds of fungi were isolated, pure-cultured, and identified to genus and often species level. Fungi with pathogenic potential were frequently isolated from surface sterilized root material. *Fusarium* was the most frequently isolated genus, from both healthy and necrotic

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root material and at every plant position. Facultatively parasitic plant pathogens are common in this genus; this class of fungi can survive and multiply saprophytically on organic substrates, but can also induce plant disease, especially when plant host defense mechanisms are lowered because of environmental stress (Nelson and others 1990). Some *Fusarium* species commonly induce both vascular wilt and root rot in susceptible plants. Other genera commonly isolated were *Alternaria*, known to cause leaf spot and twig blight, *Cephalosporium*, also capable of causing vascular wilt, and *Sclerotium*, *Rhizoctonia*, and *Pythium*, all of which can cause root rot or "damping-off" of seedlings.

As a part of these dieoff studies, soil samples were collected from the rhizosphere of shadscale and other dying shrubs, and populations of fungi closely related to *Pythium* (referred to hereafter as pythiaceous fungi) were counted on selective agar media. A very strong correlation between small secondary rootlet mortality and dieoff severity ($r = -0.99$, $P = <0.01$) and a significant correlation between number of pythiaceous fungi and dieoff severity on a site ($r = 0.64$, $P = <0.01$) was observed (fig. 1). The number of pythiaceous propagules was quite variable and ranged from 163 to 2,931 per gram of soil in sites with a low dieoff severity to 1,416 to 6,056 per gram of soil in sites with complete shadscale dieoff.

Harper and others (1996) reported on a winterfat dieoff occurring on the Desert Experimental Range in southwestern Utah. Winterfat was being replaced by halogeton in a valley bottom, the site of a known overland waterflow. In an adjacent site winterfat was recruiting successfully as openings occurred. Soil samples were collected from both the winterfat dieoff area and adjacent healthy winterfat area; half the soil was fumigated with methyl bromide, and winterfat seeds were sown in pots in the greenhouse. Results from that study (Harper and others 1996) showed that fumigation increased winterfat recruitment in halogeton-affected soil but not in soil from the healthy winterfat site.

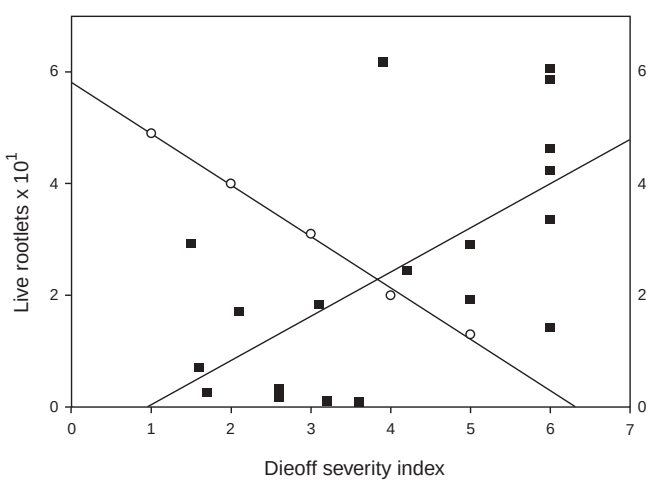

Figure 1—Correlation of dieoff severity at shadscale sites with number of live rootlets present on 30 plants excavated from each severity class and with number of pythiaceous fungi isolated from rhizosphere soil of 10 plants from each of 20 sites. Each site was ranked by averaging plant dieoff class (1 to 6) at 10-m intervals along three 100-m transects, so a site with dieoff severity of 6 consisted of all dead plants (Nelson and others 1990).

Further work on these soils carried out in our laboratory was designed to determine if density of pathogenic fungi correlated with lack of winterfat recruitment. Surface soil samples were collected in three areas: dieoff areas replaced by halogeton, dieoff areas not yet invaded by halogeton, and areas where winterfat was successfully recruiting. Soil samples were diluted and plated on two agar media, selective for either *Fusarium* species or pythiaceous species, and number of colonies was determined, with each colony representing a reproductive propagule. In winterfat dieoff soils *Fusarium* numbers were 3.4 times higher than in soils from intact winterfat areas ($P > 0.001$) (table 1). Pythiaceous fungal numbers were more than 10 times higher in winterfat dieoff soil than in intact winterfat soil ($P > 0.001$). This trend continued and intensified in areas where winterfat had been replaced by halogeton (David L. Nelson, unpublished data).

Ramsey and others (1995) presented results of a study conducted in 1992 to 1994 on an *Atriplex* seedling failure in northeastern New Mexico. A selection of an *Atriplex* hybrid of *A. canescens* X *A. obovata* repeatedly failed to become established after seeding in a nonmined site. Soil from the site and a commercial soil mix were planted with the same seed source under greenhouse conditions, and establishment was compared. Seedlings emerged in both soils, but most of the seedlings in the native soil died of "damping-off." Most seedlings in the commercial mix survived.

Diluted soil samples from the planting site and a nearby stockpile soil were plated on selective agar media designed to inhibit all but pythiaceous fungi. The planting site soil averaged 1,230 pythiaceous fungi per gram of soil, compared to 20 pythiaceous fungi per gram from the stockpile soil. Seeds treated with the fungicide Captan® (Drexel Chemical Co.) and untreated seeds were planted in a pot experiment. Seedling mortality in the soil from the failed planting site was 87 percent using untreated seed and 27.5 percent with the Captan® treated seed. A subsequent seeding at the same site using Captan®-treated seeds increased seedling survival 100-fold.

New Research

Shadscale Seedling Establishment Studies

In the course of our studies on shadscale germination biology (Garvin and others 1995; Garvin and Meyer 2003;

Table 1—Enumeration of *Fusarium* and pythiaceous fungi in soil from a winterfat dieoff site in western Utah. Numbers are fungal propagules per gram of soil.

Soil source	*Fusarium*	Pythiaceous fungi
Healthy winterfat area	517	105
Winterfat dieoff area	1,771	1,152
Halogeton invaded dieoff area	4,775	1,765

Meyer and others 1998), we carried out several field tests to evaluate seedling emergence and establishment. These studies were carried out in two western Utah valleys in 1991, 1997, and 2000. The 1991 study was conducted in northeastern Rush Valley with eight populations of shadscale fruits in emergence strips 8 ft long by 1 ft wide; each population was replicated eight times. A total of approximately 19,200 filled fruits were planted 1 cm deep. The study in 1997 consisted of four populations, planted in square-meter plots, replicated eight times, with approximately 32,000 filled fruits planted. A third study was carried out in 2000 using seed already in the seed bank, so total fruit density is not known. Emergence and establishment results are shown in table 2. In each test, a considerable fraction of seeds germinated and emerged; 3 months later only a small fraction of emerged seeds survived, and by the following spring none of the seedlings remained alive. Each time we counted seedlings we observed typical damping-off symptoms, even though soil moisture was adequate for survival.

Greenhouse Seedling Establishment of Winterfat and Shadscale

In 1999 we began a preliminary greenhouse pot study to determine the effect of different soils on seedling establishment. We collected soil (upper 5 to 10 cm) from each of 10 sites in four valley bottoms in western Utah, attempting to match weed-invaded sites with equivalent intact sites. Soil was either autoclaved to eliminate all microorganisms, treated with Banrot® (The Scotts Company) as a drench at the rate of 12 ounces per 100 gallons) or untreated. Rectangular pots (10 cm by 15 cm by 7.5 cm) were filled with soil, watered to saturation, and planted either with 25 winterfat seed or 25 shadscale seedlings germinated in Petri dishes in moist chill. Each soil treatment x species combination was replicated eight times. Seedling emergence was evaluated every 3 days initially and once a week after the first 2 weeks. After 3 months, plants were harvested by clipping at the soil line, dried, and weighed. We compared weedy and intact soils and different soil treatments using SAS PROC GLM Analysis of Variance.

The effect of fungicide treatment on plant survival and size is shown in figure 2. Autoclaved soil treatment results are similar. Winterfat seedling survival was significantly higher in fungicide treated and autoclaved soil treatments from weedy sites, but little effect was seen on survival in soil from intact sites. Most death of winterfat seedlings occurred 10 to 21 days after emergence with little additional seedling death after that point. We found no significant effect of soil treatment on shadscale seedling numbers. Percentage survival of transplants was similar in all three soil treatments.

Little difference in plant weight of winterfat was measured overall, although in most soils either autoclaving or drenching (but often not both) produced significantly greater plant growth than in untreated soil. The ratio of shadscale plant weight in fungicide treated soil compared to untreated soil from nonweedy sites was significantly increased by a factor of 2 ($P > 0.001$). No significant effect of fungicide or autoclave treatment was seen on shadscale plant weight when plants were grown in weedy soil.

Table 2—Number of seedlings emerged in early spring, established in late spring, and established 1 year later after a late fall planting.

	Early spring seedlings	Late spring seedlings	Year-old plants
Rush Valley	807	118	0
Skull Valley North	1,029	24	2
Skull Valley South	896	114	0

Shadscale Seedling Survival During Moist Chilling

A second preliminary study was carried out in a cold room and growth chamber. This study used four soil collections, two from a weed-invaded site and two from a nearby intact site in two western Utah valleys. Four different methods of fungus control, including biological control organisms, were tested. Subdue® (Ciba-Geigy) fungicide was applied at the recommended high rate as a drench; soil was steamed at 60 °C for 30 minutes; Kodiak® (commercial *Bacillus subtilis* GBO3 inoculum obtained from Gustafson) was applied to fruit before planting; and commercial *Gliocladium* inoculum (Soilguard®) from Gardens Alive! was pre-applied to fruit in combination with a half dosage of Subdue® fungicide applied as a soil drench. Afterripened shadscale fruits were planted in the rectangular pots as described in the previous study, watered to saturation, placed in closed plastic bags to maintain soil saturation, and incubated at 2 °C for 12 weeks. Treatments were replicated 15 times. Pots were removed from the cold, germinated seedlings were counted in each pot, and pots were moved to the growth chamber, set to approximate early spring temperature and light conditions. Unfortunately, the experiment was terminated prematurely due to overheating of the growth chamber and death of most seedlings, so only main effect means were analyzed statistically.

Results of the seedling count are summarized in table 3. This data is a measure of seedling emergence and survival during moist chilling. The steamed soil treatment is not shown since almost no germination occurred in any treatment. There was a strong indication in our data that shadscale seedlings may have been damaged before emergence by the high rate of Subdue® fungicide, since seedling emergence in the fungicide treated soil was only 31.7 percent of the control, and only 56 percent of emerged seedlings survived, compared with 71 to 76 percent survival in the other soil treatments. Emergence of plants grown in the soil treated with only one-half the high fungicide dosage (with SoilGuard®) was significantly less than emergence of plants grown in the untreated soil ($P > 0.05$); plant survival after emergence was not significantly reduced by the half dosage of fungicide. More than twice as many seedlings emerged and survived in soils collected from intact shadscale sites as in soils from weed-invaded sites ($P > 0.01$). No other differences between fungus control treatments could be determined.

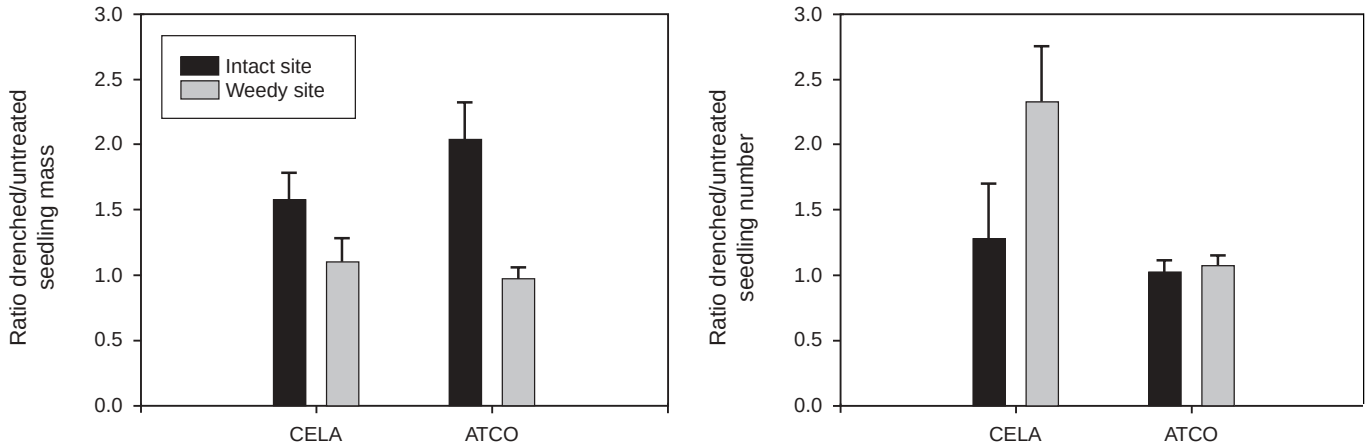

Figure 2—Means of the ratio of fungicide drench weight or seedling number to untreated values for soils from four intact sites versus soils from six weedy sites in the greenhouse pot experiment. Larger ratios indicate more effect of fungicide, with values of 1.0 indicating no effect.

Discussion

Because shadscale seed was not germinated in the presence of soil fungi in the greenhouse study, it is not surprising that seedling numbers were little affected by soil treatment. Damping-off organisms are often attracted to germinating seeds (Schroth and Cook 1964) so seedlings that might have become infected in the test soils during this period survived. Pathogens in the test soils seldom killed shadscale seedlings after emergence. Increased survival of winterfat seedlings in treated weedy soils can be interpreted to mean that a group of pathogenic fungi was suppressed by fungicide and autoclaving. The interpretation of the shadscale weight data becomes more problematic. If pathogens were responsible for inhibited plant growth we would expect that soil treatments that decrease numbers of facultative soil fungi would increase plant weight. We found this to occur in the soil from intact shadscale sites but surprisingly not in the soil from weedy sites. One interpretation might be that fungicide treatment suppressed endemic low levels of pathogens (root nibblers) and promoted more growth in intact soils but was ineffective against a different pathogen or pathogens in weedy soil. These arguments lead to the possibility of several different pathogens affecting chenopod shrubs, in both weed-invaded and intact soils, and at different stages of plant growth. Other evidence for this scenario comes from Nelson's (1990) studies, which show the presence of several facultative fungal pathogens in root and stem tissue of shadscale plants. It is difficult to test for pathogenicity of these organisms because plants must be stressed in some way to lead to the infection process.

Some likely confounding effects of autoclaving soil include the production of toxic organic compounds during heating and the increase in available nutrients due to the death of

Table 3—Mean fraction of shadscale seedling survival and number of emerged seedlings (live and dead) after 2 months in moist chilling at 2 °C in pots with soils from two intact and two weedy shadscale sites[a].

Soil source	Untreated	Fungicide	Kodiak®	SoilGuard®+1/2 F[b]	Site means	Weediness means
Fraction of surviving shadscale seedlings						
Dugway intact	0.671	0.588	0.690	0.702	0.663	
Rush intact	.658	.687	.861	.773	.745	.704a
Dugway weedy	.850	.609	.682	.792	.733	
Rush weedy	.658	.357	.628	.778	.605	.669a
Treatment means	.709ab	.560b	.715ab	.761a		
Number of emerged seedlings						
Dugway intact	70	17	71	47	51.25	
Rush intact	117	30	79	44	67.50	59.38a
Dugway weedy	40	23	22	24	27.25	
Rush weedy	38	14	43	18	28.25	27.75b
Treatment means	66.25a	21.00c	53.75ab	33.25bc		

[a]Main effect means followed by the same letter are not significantly different at the $P < 0.05$ level (LSD).
[b]1/2 F = One-half the full dosage of fungicide. See text for details on soil treatments and sources of biological control treatments.

the microbial population; these factors were not controlled in our test and probably explain some of the variability between soils and inconsistent results within soils. Another disadvantage of steaming or autoclaving soils high in clay content is apparent in our study on seedling emergence during moist chilling: the heated soils lost all structure and apparently became either toxic or impenetrable to seedlings. Soil fumigation might lead to clearer results, although fumigation, as well as autoclaving, can cause a flush of available nitrogen after soil biota are killed.

Another confounding factor is that fungicide treatment of soil may be toxic to some plant species (Leach and MacDonald 1978). If the clay fraction of the soil is lower than in agricultural soil, less fungicide is bound by the clay fraction. Conversely, if the clay fraction is higher than in most agricultural soils, more fungicide may be bound by clay particles and not available for killing fungal pathogens. Soil organic matter can also immobilize fungicide, so increased organic matter in weed-infested soils may bind more fungicide than in soils from intact shrub sites. More research needs to be carried out to discover effective rates of application of fungicide on chenopod shrubs and in different desert soils. Because we do not know which fungi are acting as pathogens, we may not have used an appropriate fungicide. We are currently engaged in studies on shadscale seeds designed to isolate possible pathogens from infected shadscale seedlings. Candidate fungi will then be tested by inoculating shadscale fruits and re-isolating the fungus from infected seedlings. We will also determine appropriate rates of fungicide application for the valley bottom soils from our study sites and test these rates for toxicity to shadscale germination and seedling stages.

The massive chenopod shrub dieoff associated with record precipitation and subsequent invasion of annual weeds has also resulted in changes in the soil. Harper and others (1996) measured increased salinity in the surface soil of halogeton-infested winterfat sites. Increased salinity probably cannot account for the death of mature shrubs, but plants in the germination and young seedling stage are far more susceptible to increased salinity, so this could be a factor in recruitment failure.

Ewing and Dobrowolski (1992) characterized soil factors such as moisture and salinity in the plant communities in Puddle Valley, UT, where shadscale dieoff was extensive in the early 1980s. They found that dead shadscale was negatively correlated with slope and elevation; the greatest density of dead shrubs was found in flat valley bottoms. Shadscale death was positively correlated with increased clay content and increased soil moisture, both conditions leading to enhancement of favorable sites for fungus proliferation. Sites with higher salinity had greater rates of survival. The leading edge of shadscale dieoff was followed from 1987 to 1989; the authors concluded that the dieoff was continuing even after precipitation levels returned to normal.

Topsoil organic matter and surface litter also increase in annual weed-infested sites, which is likely to increase the populations of facultatively parasitic fungi, such as *Fusarium* and *Pythium*. Other soil biotic changes may also occur, as shown by Evans and Belnap (1999), such as decreased nitrogenase and ammonia mineralization activity in sites with disturbed cryptobiotic crust. Belnap and Phillips (2001) found that plant pathogenic fungi increased in cheatgrass-invaded perennial grass sites in Canyonlands National Park. Bolton and others (1993) measured increased surface soil microbial biomass carbon and nitrogen, soil respiration, dehydrogenase, and phosphatase activity in cheatgrass invaded soil compared to soil under sagebrush, perennial grass, and cryptobiotic crust. The changes to soil biota and chemistry caused by annual weed invasion have only begun to be studied; effective measures to restore native communities need to consider changes within as well as above the soil.

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