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Regeneration Ecology of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* in Upland Balochistan: II. Dispersal, Predation and Soil Reserves of Seeds (Spikelets)

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Abstract: Experiments were conducted in a representative *Cymbopogon-Chrysopogon* grassland in upland Balochistan, Pakistan to determine how seed (spikelet) dispersal mechanisms, seed (spikelet) predation, and soil seed (spikelet) bank dynamics influence the regeneration of *Cymbopogon jwarancusa* and *Chrysopogon aucheri*. Spikelet dispersal occurs primarily by wind over a 2 to 3-week period in late-June/early-July. Higher densities of spikelets fell beneath conspecific plant canopies than the interspaces between plants. *Cymbopogon jwarancusa* distributed more spikelets in all microhabitats than *Chrysopogon aucheri*. Ants (*Tica verona*) were the only major spikelet predator in the study area, and they have a preference for *Chrysopogon aucheri* spikelets over *Cymbopogon jwarancusa* spikelets. Lowest soil spikelet densities for both species in all microhabitats were recorded in early-April (before seedling recruitment and spikelet dispersal), whereas highest soil spikelet densities were recorded in mid-July (after seedling recruitment and spikelet dispersal). Higher soil spikelet densities were found under plant canopies than in open interspaces, and in the upper soil depth (0-2.5 cm) than the lower soil depth (2.5-5.0 cm). In general, *Cymbopogon jwarancusa* had better soil spikelet reserves than *Chrysopogon aucheri*.

Key words: Seed morphology; seed viability; seed bank dynamics; microhabitats

Introduction

Factors that influence the regeneration of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* in grasslands of upland Balochistan, are important to researchers and managers because ecosystem-level processes are highly correlated with the behavior of these dominant species (Carney, 1989). Management and restoration of *Cymbopogon-Chrysopogon* grasslands require knowledge of seed distribution in different microhabitats, seed predation, and seed bank dynamics (Chambers and MacMahon, 1994). Seed (spikelet) dispersal mechanisms for *Chrysopogon aucheri* and *Cymbopogon jwarancusa* have been described in a related study (Ahmad *et al.*, 2000a).

Studies on seed predation indicate that both predispersal and postdispersal seed predators can influence species survival, soil seed bank dynamics, and recruitment (Schupp, 1990). Rodents, birds, and ants are the common postdispersal predators, and are commonly found in many arid regions of the world (Morton and Davidson, 1988). The effects of seed predation on the dominant species of *Cymbopogon-Chrysopogon* grasslands in upland Balochistan have not been explored, and there is a need to identify the major seed predators and their influence on seed dispersal, seed bank dynamics, and plant recruitment.

The soil seed bank plays a vital role in the recruitment of plant species after disturbances in many plant communities (Coffin and Lauenroth, 1989). Seed morphology, soil roughness, seed dispersal, and seed predators determine the input of seeds into the soil seed bank. Perennial grasses usually have a transient seed bank (Kinucan and Smeins, 1992), and livestock grazing can have a significant impact on aboveground vegetation and the soil seed bank in many grassland communities. Grazing pressure can eliminate palatable grass species by reducing seed production and seed input into the soil seed bank, and thus reducing the recruitment potential from the seed bank (O'Connor and Pickett, 1992). *Chrysopogon aucheri* is more preferred by small ruminants over *Cymbopogon jwarancusa*; however, information is lacking on the status of the soil seed bank of these species in the grasslands of upland Balochistan.

The objectives of this study were to determine: 1) patterns of seed distribution among different microhabitats, 2) loss of seeds to predators, and 3) spatial and temporal patterns of soil seed reserves in different microhabitats.

Materials and Methods

The detail of the study site is described by Ahmad *et al.* (2000a). Three transects were established across the site in a west to east direction. The first transect (500 m long) was used to study spikelet dispersal into three major microhabitats (beneath *Cymbopogon jwarancusa* canopies, beneath *Chrysopogon aucheri* canopies, and interspaces). The second transect (200 m long) was established 10 m to the north of the first transect for quantifying seed predation. Soil seed (spikelet) bank sampling was conducted on the third transect (300 m long), beginning 15 m from the east end of the first transect.

Seed (spikelet) rain of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* was quantified along the 500 m transect during the 1996 and 1997 growing seasons. Fifty points, each 10 m apart, were selected along the transect line, and at each point three spikelet traps were used, one adjacent to a *Chrysopogon aucheri* plant, one adjacent to a *Cymbopogon jwarancusa* plant, and one in the interspace between the *Chrysopogon* and *Cymbopogon* plants. Spikelet traps (modified from Schott, 1995) were placed prior to spikelet dispersal of both species. Trapped spikelets were removed from funnels at 2-week intervals over the entire dispersal period, separated by trap location, and placed in plastic bags for identification and counting.

Friedman's test for randomized blocks was used to assess differences in spikelet rain by microhabitat (Friedman, 1937). Significance of microhabitats was adjusted according to the sequential Bonferroni technique (Rice, 1989). Multiple comparisons among microhabitats were determined with Conover's test (Conover, 1980) at a 0.05 significance level.

Spikelet predation by rodents, ants, and birds was monitored at 20 selected points (10 m apart) along the 200 m transect

during the 1996 season. At each point, three different predation treatments (spikelets accessible only to rodents, spikelets accessible only to birds; and spikelets accessible only to ants) were placed under the canopy of the nearest *Chrysopogon aucheri* plant, under the canopy of the nearest *Cymbopogon jwarancusa* plant, and in the interspace between these plants. Each treatment consisted of paired petri dishes, one containing 25 triplet spikelets of *Chrysopogon aucheri* and the other containing 25 paired spikelets of *Cymbopogon jwarancusa*. Petri dishes were 10 cm in diameter and 2.5 cm deep, and had small holes in the base for drainage.

No spikelet predation by birds, rodents, or ants was observed. However, observations at the field site indicated that ants (*Tica verona*) had limited foraging activities with both species after spikelet dispersal. Therefore, to further quantify spikelet predation by ants and to assess their preferences, soil samples were collected on July 18, 1996, at five randomly located ant mounds along the same transect. At each ant mound, 10 soil samples were collected around the perimeter of the mound with a 10 cm diameter core at two depths (0-2.5 cm and 2.5-5 cm). Soil samples were passed through different-sized screens for spikelet identification and counting. Numbers of spikelets in ant mounds were converted into spikelet density/m² by calculating the total sampling area and the number of spikelets in cores on a per m² basis. Means and standard errors for *Chrysopogon aucheri* and *Cymbopogon jwarancusa* spikelets were calculated.

The 300 meter transect for seed (spikelet) bank studies was used during the 1997 growing season. Thirty points were established on this transect (10 m apart) for collecting soil samples in different microhabitats at different times of the year. Samples were taken in early April 1997 (before spikelet dispersal and seedling recruitment), mid July 1997 (after seedling recruitment and spikelet dispersal), and early September 1997 (near end of growing season). Ten of the 30 regularly selected transect points were used at each of the three sampling times. Soil samples were collected at two soil depths, 0-2.5 cm and 2.5-5.0 cm, using a 10 cm diameter soil core. At each transect point, 5 samples were taken from each of 7 major microhabitats: 1) gravel interspace, 2) soil interspace, 3) under the canopy of *Chrysopogon aucheri* plants, 4) under the canopy of *Cymbopogon jwarancusa* plants, 5) under the canopy of *Artemisia maritima* plants, 6) within the dead center of *Chrysopogon aucheri* plants, and 7) within the dead center of *Cymbopogon jwarancusa* plants. Soil samples were passed through different-sized screens to collect spikelets for identification, counting, and viability testing. Caryopsis viability was determined with 1% triphenyl tetrazolium chloride solution (Grabe, 1970). Spikelet density/m² was determined by calculating the total sampling area and the number of spikelets per core on a per m² basis. Separate analyses were used for each sampling period and for each species after pooling the sub-samples. Data were square-root-transformed prior to analysis to meet normality assumptions. The experimental design was a two-way factorial in a blocked, split-plot design. Tukey's multiple comparison test ($P < 0.05$) was used to separate spikelet density values among different microhabitats. Analyses were performed using Proc Mixed procedures in SAS Release 6.12 (SAS Institute Inc. 1996).

Results

Seed dispersal trends among microhabitats were same during 1996 and 1997 seasons. Therefore, only the results for 1997

season are presented. Initial spikelet distribution varied significantly over microhabitats for both species ($P = 0.0001$ for *Chrysopogon aucheri* and $P = 0.024$ for *Cymbopogon jwarancusa*). The numbers of trapped spikelets of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* in different microhabitats during 1997 season are presented in Figure 1. More *Cymbopogon jwarancusa* spikelets were trapped under *Cymbopogon jwarancusa* canopies than under *Chrysopogon aucheri* canopies and in interspaces. Similarly, more *Chrysopogon aucheri* spikelets were trapped under *Chrysopogon aucheri* canopies than under *Cymbopogon jwarancusa* canopies and in interspaces.

No spikelet predation was observed by rodents or birds. Ants

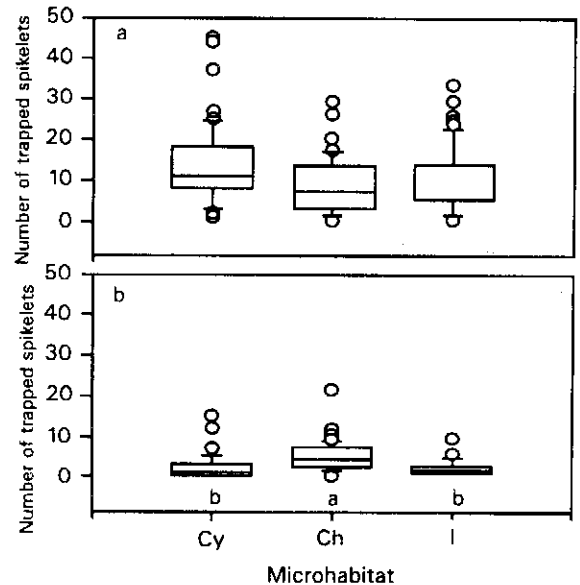


Fig. 1: Box plots showing the numbers of trapped spikelets for (a) *Cymbopogon jwarancusa* spikelets and (b) *Chrysopogon aucheri* spikelets in different microhabitats (Cy = *Cymbopogon jwarancusa* canopies, Ch = *Chrysopogon aucheri* canopies, I = interspaces) during the seed dispersal period in 1997. The horizontal line within the box is the median, the box spans the 25th-75th percentile range, the vertical lines span the 10th-90th percentile range, and circles are more extreme values. Microhabitats with different letters are significantly different ($P < 0.05$).

did not remove any spikelets of *Chrysopogon aucheri* or *Cymbopogon jwarancusa* from petri dishes; however, ants were observed carrying naturally dispersed spikelets of both species to nearby ant mounds. Ant mound soil sampling was performed on July 18, 1996, which corresponds to the soil seed bank sampling period in 1997 after seedling recruitment and spikelet dispersal. More *Chrysopogon aucheri* spikelets were recovered from ant mound soil samples than *Cymbopogon jwarancusa* spikelets (Table 1). The densities of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* spikelets in ant mounds were different from the soil seed (spikelet) bank data in a number of ways and indicate that ants buried some spikelets at deeper depths. Moreover, only the buried *Chrysopogon aucheri* spikelets were fragmented. Although the

Table 1: Mean number (\pm SE) of spikelets/m² of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* at different soil depths in ant mounds

Soil depth (cm)	<i>Chrysopogon aucheri</i>	<i>Cymbopogon jwarancusa</i>
0-2.5	1604 \pm 388	1184 \pm 134
2.5-5	2609 \pm 448	827 \pm 107

Table 2: Mean number of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* spikelets/m² (back transformed from arcsine transformed analyses) at 0-2.5 and 2.5-5.0 cm soil depths in different microhabitats before spikelet dispersal and seedling recruitment (April 3, 1997). Within columns, values with different letters are significantly different ($P < 0.05$)

Microhabitat*	<i>Chrysopogon aucheri</i>		<i>Cymbopogon jwarancusa</i>	
	0-2.5 cm	2.5-5.0 cm	0-2.5 cm	2.5-5.0 cm
Cy canopy	11.0 b	0.0 a	277 a	35.0 a
Ch canopy	91.0 a	4.0 a	124 ab	7.0 a
Cy dead center	0.7 b	0.3 a	214 a	7.0 a
Ch dead center	120.0 a	0.3 a	112 ab	2.0 a
Art canopy	13.0 b	1.0 a	153 ac	0.3 a
Gravel interspace	0.3 b	0.3 a	13 b	1.0 a
Soil interspace	0.3 b	0.0a	38 bc	2.0 a

* Abbreviations for microhabitats in Tables 2, 3, and 4 are: Cy = *Cymbopogon jwarancusa*, Ch = *Chrysopogon aucheri*, Art = *Artemisia maritima*.

Table 3: Mean number of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* spikelets/m² (back transformed from arcsine transformed analyses) at 0-2.5 and 2.5-5.0 cm soil depths in different microhabitats after seedling recruitment and spikelet dispersal (July 15, 1997). Within columns, values with different letters are significantly different ($P < 0.05$)

Microhabitat*	<i>Chrysopogon aucheri</i>		<i>Cymbopogon jwarancusa</i>	
	0-2.5 cm	2.5-5.0 cm	0-2.5 cm	2.5-5.0 cm
Cy canopy	98.0 ab	7 a	732 a	38 a
Ch canopy	208.0 ab	28 a	337 b	32 a
Cy dead center	77.0 b	18 a	368 ab	40 a
Ch dead center	249.0 a	23 a	360 ab	33 a
Art canopy	167.0 ab	46 a	488 ab	42 a
Gravel interspace	63.0 b	1 a	187 b	23 a
Soil interspace	89.0 ab	4 a	278 b	30 a

Table 4: Mean number of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* spikelets/m² (back transformed from arcsine transformed analyses) at 0-2.5 and 2.5-5.0 cm soil depths in different microhabitats near the end of the growing season (September 2, 1997). Within columns, values with different letters are significantly different ($P < 0.05$)

Microhabitat*	<i>Chrysopogon aucheri</i>		<i>Cymbopogon jwarancusa</i>	
	0-2.5 cm	2.5-5.0 cm	0-2.5 cm	2.5-5.0 cm
Cy canopy	81.0 a	9.0 a	299.0 a	44 a
Ch canopy	69.0 a	10.0 a	173.0 ab	13 a
Cy dead center	19.0 a	15.0 a	129.0 ab	2 a
Ch dead center	99.0 a	8.0 a	162.0 ab	19 a
Art canopy	110.0 a	14.0 a	350.0 a	33 a
Gravel interspace	53.0 a	6.0 a	46.0 b	14 a
Soil interspace	38.0 a	5.0 a	74.0 b	24 a

percentages of fragmented spikelets, and filled and unfilled caryopses were not quantified, most of the buried *Chrysopogon aucheri* spikelets were fragmented and without caryopses. The soil seed bank and ant mound data cannot exactly be compared with each other due to different sampling years, different sampling sites, and different spikelet production. However, ant mound soil samples provide some information about ant predation behavior and species preference.

Seed (spikelet) densities of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* varied with microhabitats and soil depths for each sampling date (Tables 2, 3, and 4). More spikelets were found in the upper (0-2.5 cm) soil depth than the lower (2.5-5.0 cm) soil depth in all microhabitats (Tables 2, 3 and 4). There were no significant differences in spikelet densities among microhabitats at the lower depth at any sampling period. Lowest spikelet densities for both species in most microhabitats were recorded in early April, before seedling recruitment and spikelet dispersal (Table 2); whereas, highest spikelets densities were recorded in mid-July, after

seedling recruitment and spikelet dispersal (Table 3). In general, spikelet densities for both species were highest under conspecific canopies and in conspecific dead centers, and lowest in heterospecific dead centers and in gravel and soil interspaces. Spikelet densities were generally intermediate under *Artemisia* canopies for *Cymbopogon jwarancusa* (Tables 2 and 3), except during the September period when they were higher than gravel and soil microhabitats (Table 4).

Discussion

For each species, higher densities of spikelets fell beneath conspecific canopies than either under the other species = canopies or in the interspaces. *Cymbopogon jwarancusa* spikelet fall was more dense in all microhabitats. This is probably related to the higher per cent cover and higher spikelet production per plant than of *Chrysopogon aucheri*. The lower densities of spikelets in interspaces is related to distance from the parent plant and abiotic factors during seed dispersal. Most species dispersed by wind and gravity distribute seeds under or near the parent plants, as in the case

of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* (Russell and Schupp, 1998). However, because of the overwhelming abundance of open gravel interspaces (70%), most spikelets still fall into open interspaces. Grasses mostly have a spatially patchy seed distribution, and this patchiness influences lateral seed movement, seed entrapment, soil seed bank reserves, and seedling recruitment and establishment (Chambers and MacMahon, 1994).

Samples around the ant mounds after spikelet dispersal indicated

higher densities of *Chrysopogon aucheri* spikelets than *Cymbopogon jwarancusa* spikelets at both depths. Ants buried the spikelets of both *Cymbopogon jwarancusa* and *Chrysopogon aucheri* at deeper depths than they naturally occur. Moreover, the buried spikelets of *Chrysopogon aucheri* were fragmented and the densities of buried spikelets differed from those in the soil seed bank. Comparison of the ant mound and the seed bank data indicates that ants have some preference for *Chrysopogon aucheri* spikelets over *Cymbopogon jwarancusa* spikelets. Different factors can influence ant preference, like nutrient content and the presence or absence of toxic compounds (Hobbs, 1985). The absence of bird and rodent predation may be related to seed structure and nutrient content. Generally, birds avoid seeds with awns (Mares and Rosenzweig, 1978).

Ant predation does appear to limit the recruitment of *Chrysopogon aucheri* but not *Cymbopogon jwarancusa* because *Cymbopogon jwarancusa* spikelets in ant mounds were not fragmented and contained caryopses. Moreover, ants are playing a more secondary dispersal role for *Cymbopogon jwarancusa* by incorporating spikelets in the soil seed bank. Ants may increase the regeneration of *Cymbopogon jwarancusa* in grasslands of upland Balochistan by increasing seed dispersal distances, burying seeds to avoid further predation, and placing seeds in more favorable microsites for better seedling establishment.

The size of the seed (spikelet) bank varied greatly with sampling period. Minimum and maximum densities were recorded in all microhabitats before seedling recruitment and spikelet dispersal and after fresh spikelet rain, respectively. Plant canopies captured and retained greater densities of spikelets than open microhabitats. This initial pattern of spikelet arrival was also confirmed from the study of spikelet dispersal into the three major microhabitats.

The soil seed bank is a function of seed morphology, roughness of the ground, seed production, seed dispersal, insect and small mammals activities, and rain intensity and frequency (Peart, 1989). Morphologically, both species have similar structures (e.g., hygroscopic awns) that should enhance the drilling of seeds into the soil. Plant canopies and their dead centers retained more seeds in all sampling periods, possibly due to the accumulation of more litter and organic matter than bare interspace surfaces (Aguar and Sala, 1997). Moreover, greater spikelet production by *Cymbopogon jwarancusa* contributed to its higher soil seed bank reserves at all sampling times.

Most of the *Cymbopogon jwarancusa* and *Chrysopogon aucheri* spikelets were found in the upper 0-2.5 cm soil layer, as with other seed-bank studies (Graham and Hutchings, 1988). Persistent and transient seed banks play a vital role in species recovery after disturbances (Grime, 1981). Perennial grasses, however, mostly have a transient rather than a persistent soil seed bank (Kinucan and Smeins, 1992). The low persistent seed bank of grasses has been related to their quick germination after dispersal under appropriate soil

moisture and temperature conditions, and their short dormancy period and low viability (Roberts, 1986). Soil seed bank data for *Cymbopogon jwarancusa* and *Chrysopogon aucheri* indicate that both species retained some viable seeds in the soil for future seedling germination and establishment.

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