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Regeneration Ecology of Chrysopogon Aucheri and Cymbopogon Jwarancusa in Upland Balochistan: I. Morphology, Viability and Movement of Seeds (Spikelets)

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Abstract: Experiments were conducted in a representative *Cymbopogon-Chrysopogon* grassland in upland Balochistan to determine how seed (spikelet) attributes and seed (spikelet) dispersal mechanisms influence the regeneration of *Cymbopogon jwarancusa* and *Chrysopogon aucheri*. *Cymbopogon jwarancusa* had more filled and viable caryopses than *Chrysopogon aucheri*. Spikelets of both species have similar morphological features. Spikelet dispersal occurs primarily by wind over a 2 to 3-week period in late-June/early-July. *Chrysopogon aucheri* has one dispersal unit, a triplet spikelet. *Cymbopogon jwarancusa* has four different dispersal units: a paired spikelet, a partial raceme, an entire raceme, and a partial inflorescence (two racemes). Mean dispersal distances of spikelets from the perimeter of the basal crown of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* plants were 94 and 79 cm, respectively. Spikelets were distributed in all directions around parent plants; however, the mean angle of dispersal for both species was toward the northeast, according to the prevailing wind direction. Spikelets of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* moved mean distances of 26 and 32 cm, respectively, from all locations on the ground surface before becoming trapped in a microhabitat. Gravel interspaces and areas beneath plant canopies were the most common microhabitats, and captured the majority of spikelets of both species.

Key words: Seed dispersal, seed morphology, seed viability

Introduction

Cymbopogon jwarancusa and *Chrysopogon aucheri* are the dominant, perennial, C_4 bunchgrasses in the arid grasslands of Balochistan, Pakistan. Sustainable production of these species depends on their continuous recruitment and proper management. Management efforts need to consider the regeneration ecology of both species under the prevailing environmental conditions. To date, however, no studies have evaluated the factors influencing the regeneration of either species.

Growing evidence indicates that the regeneration of most grass species depends, to a large degree, on the production of viable seeds, patterns of seed dispersal, seed predation, seed bank dynamics, and the presence of suitable microsites and environmental conditions for germination and seedling establishment (Aguiar and Sala, 1997; Russell and Schupp, 1998). A better understanding of these parameters will improve our knowledge of the regeneration process and how it influences plant patterns in populations or communities (Schott, 1995). Seed dispersal can reduce seed predation rates and seedling competition by dispersing seeds away from the parent plant and can provide seedling recruitment opportunities by dispersing seeds directly to favorable habitats.

The seed dispersal process typically involves two distinct phases (Chambers and MacMahon, 1994). Primary or Phase I dispersal is the movement of seeds from the parent plant to a surface, and secondary or Phase II dispersal is the subsequent movement of seeds on or into the soil surface. Plant height, seed morphology, characteristics of the surrounding vegetation, and wind conditions are some of the characteristics that determine the movement of seeds from the parent plant to a surface (Willson, 1993; Carey and Watkinson, 1993). Phase II movements are determined by site surface characteristics, seed size and shape, and animal activities (Chambers *et al.*, 1991). Lateral movement of seeds during Phase II dispersal has been recognized as a significant factor, particularly in sparse vegetation of arid and semiarid regions (Russell and Schupp, 1998). However, most seed dispersal studies rely only on the results of Phase I seed dispersal, and this has led to an incomplete understanding of seed dispersal processes (Chambers and MacMahon, 1994).

The objectives of the study were to determine: 1) the morphology and viability of seeds of *Chrysopogon aucheri* and *Cymbopogon jwarancusa*, 2) patterns of seed distribution among different microhabitats, 3) spatial patterns of dispersal of seeds from *Chrysopogon aucheri* and *Cymbopogon jwarancusa* plants to the soil surface, and 4) movement of seeds of these species on the soil surface.

Materials and Methods

Seed dispersal studies were conducted at Chiltan National Park, Hazarganji, located about 28 km south of Quetta, Balochistan. This area has been protected from livestock grazing since 1964. The park area is situated in a Mediterranean climate, with a mean annual precipitation of 250 mm. Yearly mean minimum and maximum air temperatures at the site are -7 and 38 °C, respectively (Marwat *et al.*, 1992).

A representative site was selected in the park area in terms of soils, slopes, composition of vegetation, good distribution of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* throughout the site, and presence of seven different major microhabitats (under the canopy of *Cymbopogon jwarancusa* plants, under the canopy of *Chrysopogon aucheri* plants, within dead centers of *Cymbopogon jwarancusa* plants, within dead centers of *Chrysopogon aucheri* plants, under the canopy of *Artemisia maritima* plants, gravel interspaces between plants, and soil interspaces between plants). A 200 m transect was established for characterizing seed (spikelet) dispersal unit attributes and measuring Phase I and Phase II seed (spikelet) dispersal distances and directions for *Cymbopogon jwarancusa* and *Chrysopogon aucheri*. Ten plants each of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* were characterized for inflorescence length and number of spikelets per inflorescence. Percentages of filled and viable caryopses determined for both species. Four replications of 100 spikelets for each species were measured for length (including awns), width, and mass. The same attributes were also measured for other dispersal units of *Cymbopogon jwarancusa*. Counts of filled and unfilled caryopses and viability of filled caryopses were assessed by another set of four replications of 100 spikelets for each species. Filled caryopses were placed separately in a 1% triphenyl tetrazolium chloride solution for 48 hours at room temperature (22-25 °C) in darkness, and percent viability was determined by evaluating the intensity of staining and staining patterns under a 10x lens (Grabe, 1970).

Phase I and Phase II dispersal were investigated at 20 points of 200 m transect line. For Phase I dispersal, one nearest *Chrysopogon aucheri* plant and one nearest *Cymbopogon jwarancusa* plant were picked at each of the first 10 selected points. Prior to spikelet dispersal, fluorescent powder was applied to spikelets on the marked plants at each transect point. Cheesecloth was placed on the soil surface within a 3 m radius surrounding each marked plant to entrap and retain dispersed spikelets where they initially landed. Spikelet dispersal was checked every 24 hours. After locating the marked spikelets, their direction and distance from the marked plant were measured and the spikelets were removed. The distance of a dispersed spikelet was measured from the perimeter of the basal crown of each marked plant. Prevailing wind speed was measured at different points with a hand-held anemometer at the top of plant canopies at 900 hours, 1200 hours, and 1500 hours during the spikelet dispersal period. Mean, median, and modal dispersal distances were calculated for each species. The mean spikelet dispersal direction was calculated by using circular statistical methods (Batschelet, 1981). The remaining 10 points on the transect were used for assessing Phase II dispersal. Phase II dispersal was based on the results from the Phase I dispersal study. Groups of five, marked, paired spikelets of *Cymbopogon jwarancusa* were placed 30 cm away from marked *Cymbopogon jwarancusa* plants in northeast and northwest directions, and groups of five, marked, triplet spikelets of *Chrysopogon aucheri* were placed 20 cm away from marked *Chrysopogon aucheri* plants in northeast and northwest directions. Direction and distance of individual spikelet movement were measured at 3-day intervals after placement of spikelets, until the spikelets became trapped in microhabitats or could no longer be relocated. After measuring the distance, direction, and entrapment microhabitat of trapped spikelets, they were removed and morphological features were characterized as described earlier. A 1 x 1 m quadrat that had been subdivided into a grid with 20 x 20 cm cells was used to determine the relative abundance of different microhabitats at each marked point within a 3 m radius at northeast, northwest, southeast, and southwest directions. Wind speed and direction at the ground surface were recorded in the same manner as for Phase I dispersal. Monte Carlo estimation of an exact test of Chi Square was performed using StatXact 3 for windows (Mehta and Patel, 1995) to determine the association of spikelet distribution among different microhabitats during Phase II dispersal.

Results

Chrysopogon aucheri plants had a height of 40.9 ± 0.3 cm and had 40 ± 7 culms per plant. The inflorescence is paniculate, 18.8 ± 0.2 cm in length, with 11.8 ± 0.2 spikelets. Overall, *Chrysopogon aucheri* plants produced 473 ± 91 spikelet clusters per plant. Each spikelet cluster consists of three spikelets. The middle, sessile spikelet is fertile and the two outside, pedicellate spikelets are sterile. The sessile spikelet has a hygroscopically active awn that is tightly twisted below the knee. The callus of the sessile spikelet is blunt and covered with antrorse bristles. At maturity, a triplet of spikelets usually detaches from the inflorescence.

Cymbopogon jwarancusa plants had a height of 45.8 ± 0.6 cm and had 29 ± 4 culms per plant. The inflorescence is also paniculate, 13.7 ± 0.4 cm in length. Each panicle has 4.1 ± 0.1 partial inflorescences, each comprised of two racemes subtended by a spathe. Generally, each entire raceme contains 10 to 11 paired spikelets. Overall, *Cymbopogon jwarancusa* plants produced 1184 ± 217 spikelet pairs per plant. Each spikelet pair is comprised of an upper, sterile spikelet and lower, fertile spikelet. The fertile spikelet has a hygroscopically active awn that is tightly twisted below the knee. The callus is more blunt than that of *Chrysopogon aucheri*, and is also covered with antrorse bristles. At maturity, several types of dispersal units can detach from the inflorescence, including a paired spikelet, a partial raceme, an entire raceme, and a partial inflorescence.

The typical dispersal units for *Chrysopogon aucheri* and *Cymbopogon jwarancusa* were triplet spikelets and paired spikelets, respectively. Spikelets of both species were similar in

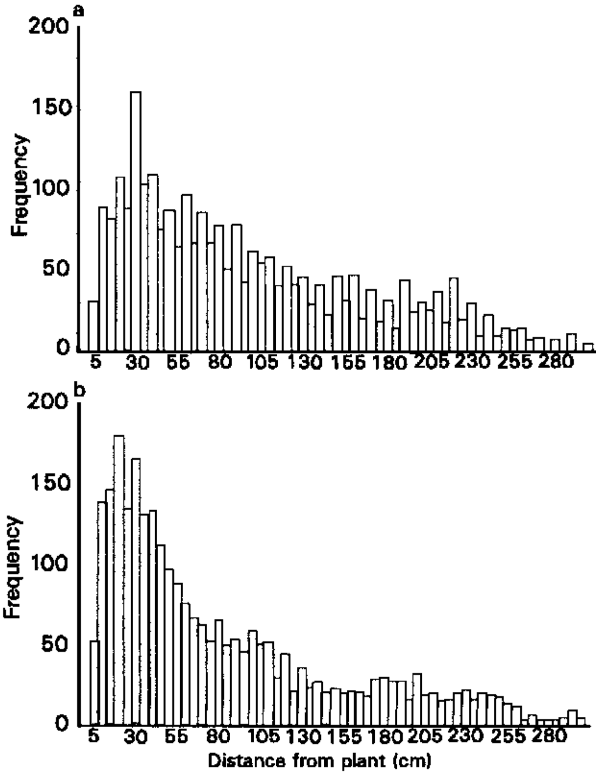

Fig. 1: Frequency distribution of dispersal distances for (a) dispersal units of *Cymbopogon jwarancusa* and (b) trip spikelets of *Chrysopogon aucheri*.

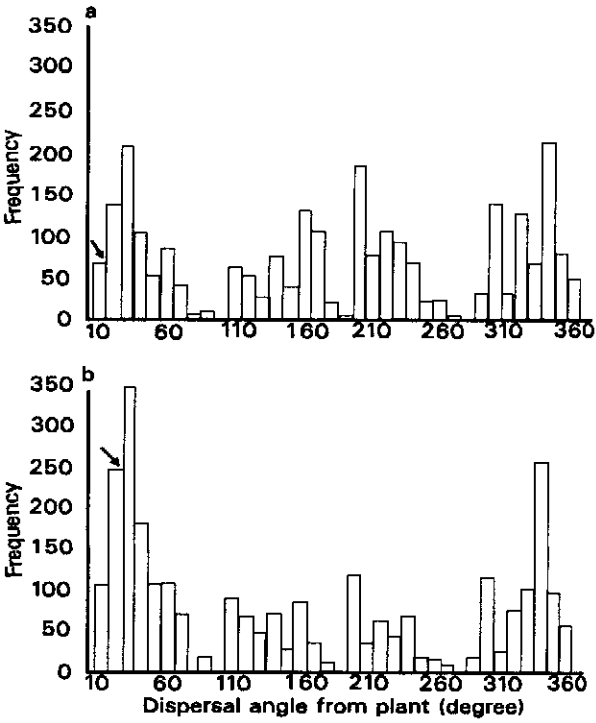

Fig. 2: Frequency distribution of dispersal directions for (a) dispersal units of *Cymbopogon jwarancusa* and (triplet spikelets of *Chrysopogon aucheri* around the parent plants. Arrow indicates the mean dispersal ang

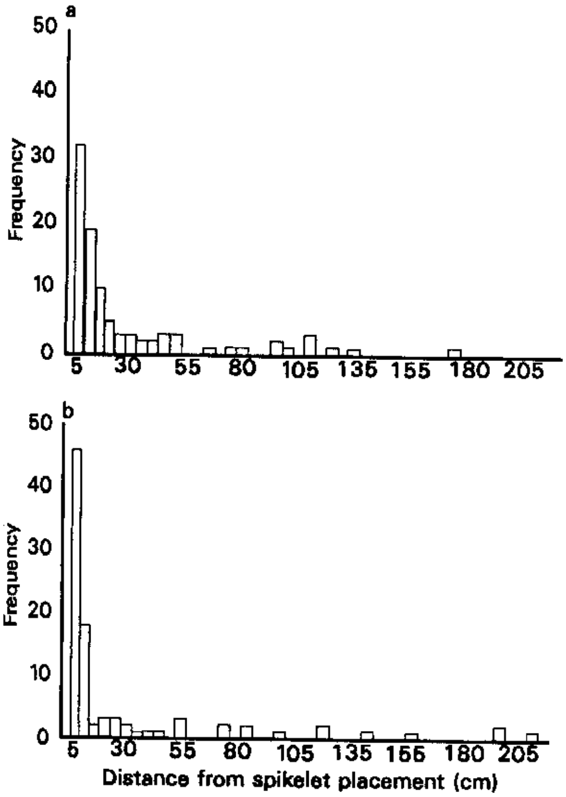

Fig. 3: Frequency distribution of dispersal distances for (a) paired spikelets of *Cymbopogon jwarancusa* and (b) triplet spikelets of *Chrysopogon aucheri* in northeast and northwest directions during Phase II dispersal.

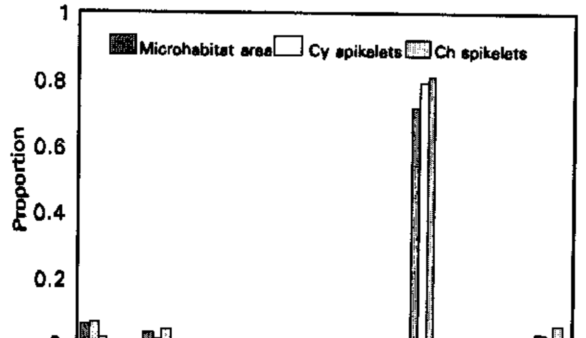

Fig. 4: Proportion of microhabitat area and proportion of trapped spikelets of Cy (*Cymbopogon jwarancusa*) and Ch (*Chrysopogon aucheri*) in different microhabitats during Phase II spikelet movement. Cy = *Cymbopogon jwarancusa* canopy, Ch = *Chrysopogon aucheri* canopy, Cyd = *Cymbopogon jwarancusa* dead center, Chd = *Chrysopogon aucheri* dead center, Art = *Artemisia maritima* canopy, Gr = gravel interspace, So = soil interspace, Other = beneath plant canopies other than Cy, Ch, and Art, and in litter

width; however, paired spikelets of *Cymbopogon jwarancusa* were shorter in length, heavier, and had less eccentricity (length:width ratio) than those of *Chrysopogon aucheri*. Partial racemes, entire racemes, and partial inflorescences of *Cymbopogon jwarancusa* were heavier, longer, and wider than paired spikelets. Partial

Table 1: Mean (± SE) mass, length, width, and length: width (eccentricity) ratio of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* dispersal units collected in 1997

Species	Mass (mg)	Length (mm)	Width (mm)	Length: width ratio
Chrysopogon aucheri				
Triplet spikelet	2.3±0.0	27.8 ± 0.1	2.0 ± 0.0	13.9±0.1
Cymbopogon jwarancusa				
Paired spikelet	3.3 ± 0.0	16.7 ± 0.1	2.1 ± 0.0	7.9+0.0
Partial raceme	7.5 ± 0.1	21.0 ± 0.1	3.0 ± 0.0	7.0±0.0
Entire raceme	12.5 ± 0.4	25.0 ± 0.1	3.0 ± 0.0	8.3±0.0

Table 2: Percent (mean ± SE) unfilled caryopses and viable/nonviable filled caryopses of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* seeds

Species	Unfilled caryopses	Nonviable filled caryopses	Viable filled caryopses
Chrysopogon aucheri	43 ± 2	7 ± 1	50 ± 3
Cymbopogon jwarancusa	20 ± 3	17 ± 3	63 ± 5

Table 3: Mean (± SE) median, and modal dispersal distance of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* dispersal units from parent plants to the ground surface

Species	Mean dispersal distance (cm)	Median dispersal distance (cm)	Modal dispersal distance (cm)
Chrysopogon aucheri			
Triplet spikelet	79.9 ± 1.3	55.0	20.0
Cymbopogon *jwarancusa*			
Paired spikelet	94.3 ± 1.5	76.0	30.0
Partial raceme	101.9 ± 3.4	87.0	70.0
Entire raceme	71.1 ± 6.0	45.0	30.0
Partial inflorescence	71.8 ± 11.8	51.0	80.0

Table 4: Mean wind velocity (" SE) at the top of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* plants at different times during the Phase I dispersal period.

Species	Wind velocity (Km/h) 900 hours	1200 hours	1500 hours
Cymbopogon jwarancusa	7.3 ± 0.2	9.3 ± 0.4	10.3 ± 0.4
Chrysopogon aucheri	6.4 ± 0.2	8.6 ± 0.3	9.4 ± 0.4

inflorescences of *Cymbopogon jwarancusa* had less eccentricity than paired spikelets, partial racemes, and entire racemes (Table 1). *Cymbopogon jwarancusa* had more filled and viable caryopses than *Chrysopogon aucheri* (Table 2).

Mean, median, and modal distances of dispersal units from the perimeter of the basal crown of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* plants are presented in Table 3. Modal dispersal distances of *Cymbopogon jwarancusa* paired spikelets and *Chrysopogon aucheri* triplet spikelets were within a 30 cm and 20 cm radius, respectively, of their parent plants. A few dispersal units moved up to 300 cm from the marked plants (Fig. 1a and 1b).

Dispersal units were distributed in all directions around parent plants; however, the mean angle of dispersal for both species was in a northeast direction. The mean angle of dispersal was 12.6° for *Cymbopogon jwarancusa* and 21.0° for *Chrysopogon aucheri* (Fig. 2a and 2b). Winds were primarily towards the north and northwest during the dispersal period which only roughly corresponds to the mean direction of dispersal. Mean wind velocity across all sampling times was higher at the top of the taller *Cymbopogon jwarancusa* plants than the shorter *Chrysopogon aucheri* plants (Table 4). A maximum wind velocity of 30.4 Km/h was recorded at the top of the plant canopies during Phase I dispersal.

Mean, median, and modal dispersal distances of both species during Phase II dispersal are presented in Table 5. Spikelets of *Chrysopogon aucheri* moved a maximum mean distance of 31.6 cm whereas spikelets of *Cymbopogon jwarancusa* moved a maximum mean distance of 26 cm before they were trapped in a microhabitat (Table 5). The modal distance category for both *Cymbopogon jwarancusa* and *Chrysopogon aucheri* spikelet dispersal before becoming trapped was the 0-5 cm category. A few spikelets moved more than 100 cm from their places of initial placement (Fig. 3a and 3b). Spikelets of both species moved in all directions along the ground surface, depending on wind directions and proximity to plants. However, the mean dispersal angle for

Table 5: Mean (± SE), median, and modal dispersal distance and angle of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* spikelets on the ground after being pl northeast and northwest of plants of both species

Species	Initial spikelet position in dispersal relation to plant	Mean dispersal distance (cm)	Median dispersal distance (cm)	Modal dispersal distance (cm)	Dispersal angle (degrees)
Chrysopogon aucheri					
	NE	19.4 ± 5.0	6.0	5.0	37.3°
	NW	31.6 ± 7.9	4.5	4.0	12.1°
Cymbopogon jwarancusa					
	NE	26.0 ± 5.2	7.0	3.0	42.2°
	NW	22.8 ± 4.7	11.5	3.0	21.1°

both species was northeast (Table 5).

Again, this only roughly corresponds to wind direction of the ground surface which was mostly to the north and northwest. Mean wind velocity at the ground surface for both species combined was 1.9 ± 0.1, 2.5 ± 0.1, and 3.0 ± 0.1 Km/h respectively, at 900 hours, 1200 hours, and 1500 hours during Phase II dispersal. Maximum wind velocity at the ground surface was 6.8 Km/h. The morphological attributes of the trapped spikelets were similar to those described in Table 1.

Neither species showed a significant ($P > 0.05$) association for spikelet distribution among different microhabitats. The gravel microhabitat occupied the highest proportional area and had the highest numbers of spikelets of both species (Fig. 4). Dead centers of *Cymbopogon jwarancusa* and *Chrysopogon aucheri*, and soil interspaces occupied the lowest proportional area and had lower numbers of spikelets than other microhabitats (Fig. 4).

Discussion

Spikelets of both species bear hygroscopic awns and antrorse bristles. Hygroscopic awns and forwardly directed antrorse bristles help seed drilling and lodging into cracks and other microsites (Peart, 1979). *Chrysopogon aucheri* has better entrapment characteristics in cracks than *Cymbopogon jwarancusa* due to its more pointed callus.

Entire racemes and partial inflorescences of *Cymbopogon jwarancusa* have greater mass than paired and triplet spikelets of *Cymbopogon jwaranusa* and *Chrysopogon aucheri*, respectively. This higher mass can increase wing loading and reduce the dispersal distance by wind (Ernst *et al.*, 1992). *Cymbopogon jwarancusa* dispersal units had less eccentricity (length:width ratio) than *Chrysopogon aucherei*, and this may affect their horizontal movement on the soil surface. Chambers *et al.* (1991) observed that length:width ratio of different forb and grass species was highly correlated with entrapment characteristics at smaller soil particle sizes. However, no single seed attribute determines dispersal characteristics. A combination of different attributes of dispersal units determines the behavior of seed movement, entrapment, and germination (Rabinowitz and Rapp, 1981).

Cymbopogon jwarancusa has the potential to produce more filled and viable seeds than *Chrysopogon aucheri* (Saleem, 1990). Both species contain male (sterile) spikelets and bisexual (fertile) spikelets; however, the proportion of sterile spikelets is higher in *Chrysopogon aucheri* plants. High sterility of *Chrysopogon aucheri* may be another reason for its lower percentage of filled and viable seeds (Hussain *et al.*, 1980). High viable seed production of *Cymbopogon jwarancusa* may increase its regeneration ability under variable environmental conditions in the arid grasslands of upland Balochistan.

Chrysopogon aucheri and *Cymbopogon jwarancusa* disperse their dispersal units immediately after maturity, mostly in mid-June, and continue for two to three weeks, depending upon the wind and other environmental conditions such as rainfall. Overall, *Cymbopogon jwarancusa* spikelets moved farther from the perimeter of the basal crown of parent plants than *Chrysopogon aucheri* spikelets. The addition of fluorescent powder increased the mass of *Cymbopogon jwarancusa* and *Chrysopogon auch* spikelets by 6% and 5%, respectively, and probably had onl negligible effect on dispersal. *Cymbopogon jwarancusa* pai spikelets are heavier than *Chrysopogon aucheri* triplet spikel whereas other morphological characteristics of both species similar. *Cymbopogon jwarancusa* paired spikelets and par racemes moved farther from the perimeter of the basal crown parent plants compared to entire racemes and par inflorescences. The low mean dispersal distance of entire racem and partial inflorescences is related to their heavy ma *Cymbopogon jwarancusa* plants are slightly taller (46 cm) th *Chrysopogon aucheri* plants (41 cm). Plant height appears to h contributed to a greater mean dispersal distance for pai spikelets and partial racemes of *Cymbopogon jwarancusa* due higher wind velocities at the top of its plant canopies. Ma studies note the importance of plant height in seed disper (Carey and Watkinson, 1993; Chambers and McMahon, 199 *Cymbopogon jwarancusa* and *Chrysopogon aucheri* spikelets w dispersed in all directions around parent plants. However, m spikelets were dispersed towards northeast and northw directions roughly corresponding to prevailing winds. T dispersal pattern can influence spikelet distribution into differ microhabitats.

Mean Phase II dispersal distances of *Cymbopogon jwarancusa* a *Chrysopogon aucheri* were less than mean Phase I disper distances. Mean spikelet movements of both species from locations was less than 32 cm from the initial placement locati Secondary redistribution of spikelets, or their horizontal a vertical movements on and in the soil, depends on dispersal u morphological characteristics, physical forces, soil particle si and animal activities (Chambers *et al.*, 1991; Aguiar and Sa 1997). Both *Cymbopogon jwarancusa* and *Chrysopogon auch* have hygroscopic awns that may drill spikelets into the s increasing their chances for germination and seedli establishment. *Chrysopogon aucheri* spikelets have larger aw than *Cymbopogon jwarncusa* spikelets. This resulted in a grea length:width ratio for *Chrysopogon aucheri* spikelets. Se length:width ratio (Chambers and MacMahon 1994) and s particle size (Chambers *et al.*, 1991) are also important fact influencing seed movement and seed entrapment. Althou *Chrysopogon aucheri* spikelets have a greater length:width rat they also have a more pointed callus that may enhance entrapme into cracks and depressions. Spikelets of both species w trapped quickly in depressions, cracks, and gravel compared partial racemes, entire racemes, and partial inflorescences *Cymbopogon jwarancusa*.

Spikelets of both species redistributed randomly during Phas movement on the ground surface and no association was detect between spikelet distribution and microhabitats. The gra microhabitat trapped a higher proportion of spikelets of bo species due to its higher proportional area than oth microhabitats. Plant canopies were also good microhabitats trapping spikelets due to the accumulation of some litter under t canopies. Soil interspaces trapped lower proportions of spikel due to their lower proportional areas and absence of litter. De centers of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* had the lowest spikelet distribution during Phase II movement, and it appears that the accumulation of spikelets in these microhabitats mainly depends on Phase I dispersal patterns. The densities of accumulated seeds in a particular microhabitats may influence other density-dependent processes like competition, predation, and herbivory (Russell and Schupp, 1998).

Phase II dispersal findings for *Cymbopogon jwarancusa* and *Chrysopogon aucheri* emphasize the importance of quantifying both Phase I and Phase II dispersal studies for a better understanding of dispersal processes in plant communities. From Phase II seed dispersal, it appears that wind plays a moderate role for the secondary movement of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* spikelets. Surface flow from monsoon rains can result in greater Phase II dispersal for both species.

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