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Regeneration Ecology of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* in Upland Balochistan: III. Effects of Precipitation and Seedbed Microhabitat on Seedling Recruitment

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Abstract: A number of seven microhabitats evaluated for seedling establishment were: under the canopy of *Chrysopogon aucheri* plants, under the canopy of *Cymbopogon jwarancusa* plants, within dead centers of *Chrysopogon aucheri* plants, within dead centers of *Cymbopogon jwarancusa* plants, under the canopy of *Artemisia maritima* plants, gravel interspaces between plants, and soil interspaces between plants. Seedling emergence and establishment were evaluated under the natural precipitation regime of the 1997 growing season and a simulated, above-normal precipitation regime. Soil moisture and soil temperature data were recorded during the entire growing season. Above-normal precipitation increased the density of emerged seedlings for both species in all microhabitats. *Cymbopogon jwarancusa* had higher seedling densities than *Chrysopogon aucheri*. Monsoon rains in late July 1997 enhanced emergence of both species from recently dispersed seeds. Seedlings of both species emerged after monsoon rains but did not survive to the end of the growing season. Gravel interspaces were suitable microhabitats for seedling development, possibly due to the vertical entrapment of dispersal units and reduced competition from more distant, established plants. Above-normal precipitation did not have a significant effect on tiller development for either species. *Cymbopogon jwarancusa* seedlings developed more tillers per plant than *Chrysopogon aucheri* seedlings.

Keywords: Germination, soil seed bank, seedling establishment, safe site, seedbed ecology.

Introduction

Plant establishment by seedling recruitment, the dominant type of regeneration for most grass species in rangeland environments, is only successful when plant requirements for seed germination, seedling establishment, and subsequent growth are matched with the micro environmental factors of the seedbed (Harper, 1977). Safe sites, or favorable micro sites of a particular growing area, rather than total number of available seeds often determine the potential for seedling recruitment (Young, 1988). Favorable water and temperature conditions for germination and establishment on or near the surface are associated with surface-soil micro topological features such as cracks, depressions, rocks/gravel, plant litter, and proximity to neighboring vegetation (Chambers *et al.*, 1990). Different micro sites can also differ in terms of nutrient availability, seed predators, and pathogens (Schupp and Frost, 1989), which can also affect germination and establishment (Schupp, 1995).

A few detailed studies have determined the types of micro sites and environmental conditions that are necessary for germination and establishment of a limited number of species on semiarid grasslands (Winkel *et al.*, 1991). A recent study has investigated the influence of gap disturbances and types of micro sites on the establishment of a dominant grass species in a semiarid grassland (Aguilera and Lauenroth, 1995). No such studies have been conducted for *Cymbopogon jwarancusa* and *Chrysopogon aucheri*, the dominant grass species in upland Balochistan. Only one greenhouse study has described the germination and seedling development of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* (Saleem, 1990), but this information is not readily applicable to the variable environmental conditions found in the field. The objective of this field study was to determine how different microhabitats and precipitation regimes influence the recruitment of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* seedlings from the soil seed bank in a representative *Chrysopogon-Cymbopogon* grassland in upland Balochistan.

Materials and Methods

The study was conducted at the Chiltan National Park, Hazarganji, Quetta. The detail of the study site is described by Ahmad *et al.* (2000a). The seven microhabitats described above were evaluated for their potential in the recruitment of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* seedlings from the soil seed bank. An above-normal spring precipitation treatment (irrigated) was simulated with a sprinkler system in addition to the natural spring precipitation treatment (control) that occurred in 1997. Above-normal precipitation for April and May 1997 was patterned after the precipitation regime during April (148 mm) and May (29 mm) 1983 at the Sumungli station, about 40 km from the field site. The amount of supplemental water applied was determined by subtracting the current precipitation (1997) from the above-normal precipitation (1983) for each week. Emerged seedlings in the above-normal precipitation treatment were exposed to ambient precipitation for the remainder of the 1997 growing season.

Experimental plots were established along a 240 m transect oriented in a west to east direction. Sixteen points, 15 m apart, were marked on this transect line and paired 5 x 5 m plots were established at each point. Plots in a pair were 10 m apart, one 5 m on each side of the transect line. Precipitation treatments (natural or above-normal) were randomly assigned to plots in a pair. Ten points on the transect were used for evaluating seedling emergence, survival, and development in different microhabitats, three for measuring soil moisture content, and three for measuring soil temperature.

A 1 x 1 m quadrat that had been subdivided into grid with 20 x 20 cm cells was used to determine the relative abundance of different microhabitats in each 5 x 5 m plot. Soil samples for each microhabitat were analyzed for soil textural class, pH, organic matter, nitrogen, phosphorus, and potassium. Soil water content was measured by the gravimetric method over the 1997 season at two depths (0-2.5 cm, 5-10 cm). Soil samples were collected 24 hours after supplemental irrigation treatments in April, May, and early, mid and late June, and at the end of July after monsoon rains. Soil temperatures were measured by using thermocouples attached to a hand-held digital

thermometer. Thermocouples were placed at depths of 2.5 cm and 10 cm in each microhabitat in each plot. Soil temperatures were measured after each supplemental irrigation at 800 hours and 1400 hours, and then at 15-day intervals up to the end of July 1997.

Emerged seedlings and survived seedlings at the end of the season for each species in each plot were converted into a density/m² value by dividing the number of seedlings by the area (m²) occupied by each microhabitat in each plot. Data for emergence density, both in the spring and after monsoon rains, and density of surviving spring seedlings were analyzed with nonparametric tests using Friedman's test (Friedman, 1937). Multiple comparisons among microhabitats were determined with Conover's test (Conover, 1980) at the 0.05 significance level. The significance level for microhabitats was evaluated according to the sequential Bonferroni technique (Rice, 1989) for both species. Friedman tests were computed using the rank and GLM procedures in SAS Release 6.12 (SAS Institute Inc. 1996).

Effects of precipitation treatment (natural vs. above-normal) on seedling density in the spring, effects of emergence season (spring vs. monsoon emergence) on seedling density, and effects of precipitation treatments (natural vs. above-normal) on the density of survived seedlings at the end of the season, were assessed with the Wilcoxon Signed Rank Test using SYSTAT release 7.0 (Wilkinson, 1997). Differences among microhabitats in the proportion of seedlings that survived to the end of the first growing season were assessed either with a Monte Carlo estimation, or in the case of small sample sizes with exact P-values for a Chi Square test. The exact P-values for a Chi Square test or the Monte Carlo estimation of an exact test for unordered R x C contingency tables was performed using StatXact 3 for windows (Mehta and Patel, 1995). The effect of precipitation treatment on the proportion of seedlings that survived to the end of the first growing season for each seedling type and each microhabitat was assessed separately by exact P-values for a Chi Square test (Mehta and Patal, 1995).

The effect of precipitation treatments on the height of surviving *Cymbopogon jwarancusa* seedlings in the gravel microhabitat was evaluated using a one-way analysis of variance in a randomized block design with subsamples. Plant height data of surviving *Chrysopogon acheri* seedlings were assessed using descriptive statistics.

Soil moisture data were analyzed separately for each sampling time by using a three-way factorial design in a split-split plot design while soil temperature data for each sampling time were analyzed with four-way factorial in a split-split-split plot design.

Tukey's multiple comparison test was performed to check moisture and soil temperature differences among different microhabitats. Data were analyzed using Proc Mixed procedure in SAS Release 6.12 (SAS Institute Inc. 1996).

Results

The 1997 growing season had comparatively favorable rains receiving both spring and monsoon rains (Fig. 1). A total of 33.8 mm and 16 mm of precipitation were received during April and May, respectively. Monsoon rains at the end of July (33.8 mm) promoted the germination of recently dispersed seeds of several species.

Soils in the seven microhabitats had similar physical and chemical characteristics (Table 1). All soils, including the soil under the gravel surface layer in the gravel interspace microhabitat, had a sandy clay loam texture. The diameter of the gravel particles in the gravel interspace microhabitat ranged from 1.1 to 4.2 cm. Four typical periods (before spring seedling emergence, during spring seedling emergence, during the dry season after cessation of supplemental irrigation, and late summer monsoon emergence) were picked to show soil moisture trends among different microhabitats and precipitation treatments (Figs 2 to 6). Substrate moisture content was significantly higher in the above-normal precipitation treatment than in the natural precipitation treatment after the first irrigation but not at any other date (Fig. 2). There were no significant differences in moisture content among microhabitats except for the May 7 sampling time when gravel interspaces had significantly higher moisture contents than gravel interspaces (Fig.4). Differences between moisture contents at two sampling depths were significant after the first irrigation (Fig. 2), but not at any other time. Means for the precipitation treatment x microhabitat x depth interaction were picked to show moisture content trend among different microhabitats at different depths for each sampling time (Figs 3 to 6).

The same periods were picked to show the temperature trends among different microhabitats. Soil temperature was significantly lower in the above-normal precipitation plots than in the natural precipitation plots after the first supplemental irrigation but not at any other time. Sampling depth and sampling time were significant for all sampling dates, whereas microhabitat was significant only after the first supplemental irrigation and after monsoon rains but not at any other time. Means for the microhabitat x time interaction were picked to show the soil temperature trends among different microhabitats for each sampling time (Figs 7 to 10). Soil temperatures in all microhabitats on all dates had higher temperatures at 1400 hours than at 800 hours.

Table 1: Soil characteristics in different microhabitats.

| Microhabitat * | Clay (%) | Silt (%) | Sand (%) | Textural class | pH | Organic matter | Nitrogen (%) | Phosphorus (ppm) | Potassium (mg/l) |
|-------------------|----------|----------|----------|-----------------|-----|----------------|--------------|------------------|------------------|
| Cy canopy | 20 | 20 | 60 | Sandy clay loam | 7.6 | 2.25 | 0.15 | 4.0 | 3.0 |
| Ch canopy | 20 | 23 | 57 | Sandy clay loam | 7.3 | 1.97 | 0.07 | 4.7 | 2.9 |
| Cy dead Center | 20 | 20 | 60 | Sandy clay loam | 8.4 | 2.44 | 0.04 | 5.8 | 2.9 |
| Ch dead center | 20 | 18 | 62 | Sandy clay loam | 7.4 | 2.96 | 0.14 | 5.5 | 2.3 |
| Art canopy | 20 | 23 | 57 | Sandy clay loam | 7.6 | 2.40 | 0.06 | 5.2 | 2.7 |
| Gravel interspace | 20 | 20 | 60 | Sandy clay loam | 8.2 | 2.13 | 0.17 | 4.8 | 4.2 |
| Soil interspace | 20 | 24 | 56 | Sandy clay loam | 7.6 | 1.89 | 0.14 | 3.8 | 4.0 |

* Cy = *Cymbopogon jwarancusa*, Ch = *Chrysopogon acheri*, Art = *Artemisia maritima*

The overall per cent cover of different microhabitats in the seedling establishment plots were: 1) *Cymbopogon jwarancusa* plant canopies, 10.3%; 2) *Chrysopogon aucheri* plant canopies, 6%; 3) *Cymbopogon jwarancusa* dead centers, 4.4%; 4) *Chrysopogon aucheri* dead centers, 0.6%; 5) *Artemisia maritima* plant canopies, 3.3%; 6) gravel interspaces between plants, 70.3%; and 7) soil interspaces between plants, 5%.

Densities of emerged seedlings of both species were significantly influenced by microhabitat type and precipitation treatment ($P < 0.05$) in the spring. Densities of emerged seedlings of *Cymbopogon jwarancusa* were significantly higher under *Cymbopogon jwarancusa* canopies and in gravel and soil interspaces than in other microhabitats in the natural precipitation treatment (Fig. 11 a). *Cymbopogon jwarancusa* seedling emergence was higher in soil interspaces than in other microhabitats in the above-normal precipitation treatment (Fig. 11 b). Densities of emerged seedlings of *Chrysopogon aucheri* were significantly higher under *Chrysopogon aucheri* canopies and in gravel interspaces compared to other microhabitats in both natural precipitation and above-normal precipitation treatments (Fig. 12 a and b).

Microhabitat also had a significant influence on the densities of emerged seedlings for *Cymbopogon jwarancusa* and *Chrysopogon aucheri* after monsoon rains in late July (Fig. 13 a and b). Seedling emergence for both species was significantly greater in soil interspaces than in all other microhabitats. *Cymbopogon jwarancusa* seedling emergence was generally lowest under canopies and in dead centers of *Chrysopogon aucheri* plants, while *Chrysopogon aucheri* seedling emergence was generally lowest under canopies and in dead centers of *Cymbopogon jwarancusa* plants. Densities of emerged seedlings of both species were significantly ($P < 0.05$) higher in almost all microhabitats after monsoon rains than after spring rains. However, none of the seedlings that emerged after monsoon rains survived until the end of the growing season in any of the microhabitats.

In contrast, seedlings of both species that emerged after spring rains did survive until the end of the 1997 growing season in at least some microhabitats in both natural and above-normal precipitation treatments (Figs 14 and 15). Microhabitats had a significant influence on the density of surviving seedlings for *Cymbopogon jwarancusa* only in the natural precipitation treatment. The density of surviving *Cymbopogon jwarancusa* seedlings was significantly greater in gravel interspaces than in other microhabitats in the natural precipitation treatment (Fig. 14 a). Densities of surviving *Cymbopogon jwarancusa* seedlings did not differ significantly among microhabitats in the above-normal precipitation treatment, although there appeared to be greater densities in soil and gravel interspaces than in other microhabitats (Fig. 14 b). Few seedlings of *Chrysopogon aucheri* survived, and there were no significant differences in densities of surviving seedlings among microhabitats in either natural or above-normal precipitation treatments (Fig. 15 a and b). There were no significant differences ($P > 0.05$) between the natural precipitation treatment and above-normal precipitation treatment in densities of surviving seedlings of either species at the end of the growing season.

Microhabitats differed significantly in the proportion of surviving *Cymbopogon jwarancusa* seedlings in both natural and above-normal precipitation treatments and in the proportion of surviving *Chrysopogon aucheri* seedlings only in the above-normal precipitation treatment. A greater proportion of *Cymbopogon jwarancusa* seedlings survived in gravel interspaces than in other microhabitats in natural and above-normal precipitation treatments (Fig. 16). Only gravel microhabitats had a significantly higher proportional survival for *Cymbopogon jwarancusa* in above-normal than in natural precipitation treatments (Fig. 16). Proportional survival of *Chrysopogon aucheri* seedlings was greatest under

Artemisia maritima canopies and in gravel interspaces in the above-normal precipitation treatment, and in soil interspaces in the natural precipitation treatment (Fig. 17). Natural and above-normal precipitation treatments did not differ significantly in proportional survival for either species.

Only the *Cymbopogon jwarancusa* canopy, and gravel and soil interspace microhabitats had enough surviving *Cymbopogon jwarancusa* seedlings to monitor seedling development, and there were no significant differences in the number of tillers per seedling among microhabitats in either natural or above-normal precipitation treatments. Surviving seedlings developed 2.0 ± 0.7 (mean \pm SE) tillers in both precipitation treatments by the end of the growing season. Surviving *Chrysopogon aucheri* seedlings did not develop beyond the one tiller stage in any microhabitat. Plant heights of surviving seedlings in the gravel microhabitat did not differ significantly between natural and above-normal precipitation treatments. Surviving seedlings of both species had a height of 3.0 ± 0.6 cm (mean \pm SE) when averaged across microhabitats and precipitation treatments.

Discussion

Seedlings of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* emerged at the same time in almost every microhabitat under natural and simulated, above-normal spring precipitation regimes in April and May 1997, and after monsoon rains in late July 1997. There were, however, differences in the favorableness of microhabitats for the survival and seedling development of both species. During spring, *Chrysopogon aucheri* seedlings generally emerged in greater numbers under the canopies of conspecific plants and in gravel interspaces, and *Cymbopogon jwarancusa* seedlings generally emerged in greater numbers in soil and gravel interspaces and under the canopies of conspecific plants. The lowest densities of emerged seedlings of *Chrysopogon aucheri* were observed under the canopies and in the dead centers of *Cymbopogon jwarancusa* plants. Similarly, the lowest densities of emerged seedlings of *Cymbopogon jwarancusa* were found under the canopies and in the dead centers of *Chrysopogon aucheri* plants. In general, density and proportional survival of spring-emerged seedlings of both species were greatest in gravel and soil interspaces near the end of the growing season in September 1997. After monsoon rains in late July 1997, a second, large cohort of seedlings for each species emerged in greatest numbers in soil interspaces, followed by microhabitats under the canopies of conspecific plants, and microhabitats under *Artemisia maritima* canopies and in gravel interspaces. All of the seedlings in these second cohorts died by the end of the growing season.

The favorableness of microhabitats for seedling emergence and survival is also related to several environmental factors. During this experiment, natural and simulated above-normal precipitation were at least two and four times higher, respectively, than long-term mean precipitation during the spring seedling emergence period (April and May). According to long-term meteorological analysis, these natural and above-normal precipitation amounts that promoted spring seedling emergence occur with about 10% and less than 10% probability, respectively (Keatinge and Rees, 1988). These precipitation events greatly increased moisture availability in upper soil layers in all microhabitats during the spring seedling emergence period. The above-normal precipitation treatment had overall higher densities of emerged seedlings of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* than the natural precipitation treatment. As the season progressed through the relatively dry months of June and July, soil moisture became very limiting, resulting in seedling mortality in all microhabitats. More seedlings of both species survived in gravel and soil interspaces than in other microhabitats; however, available

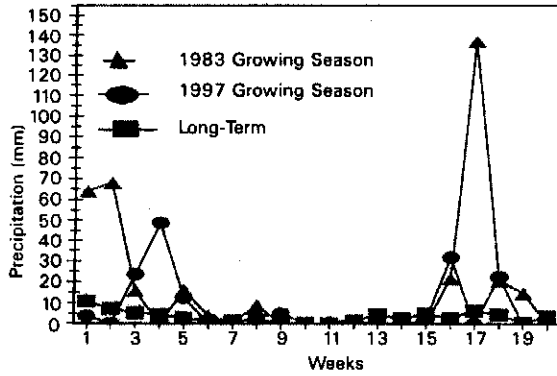


Fig. 1: Weekly precipitation from April 1 (week 1) to August 30 (week 20) for the 1983 growing season, 1997 growing season, and the long-term (average over 34 growing seasons).

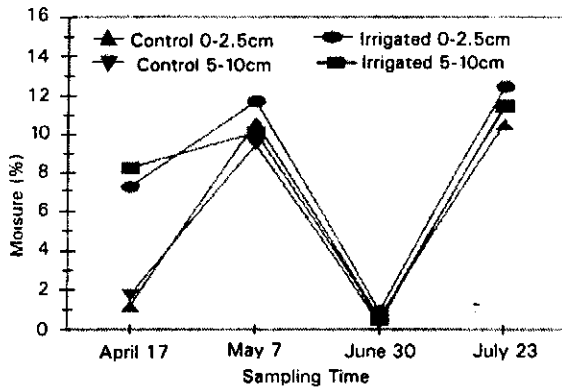


Fig. 2: Percent moisture content at 0-2.5cm and 5-10 depths in natural (control) and above-normal (irrigated) precipitation treatments (across all microhabitats). Soil moisture content was significantly ($P < 0.05$) higher in the (irrigated) above-normal precipitation treatment after first supplemental water before seedling emergence on April 17, 1997.

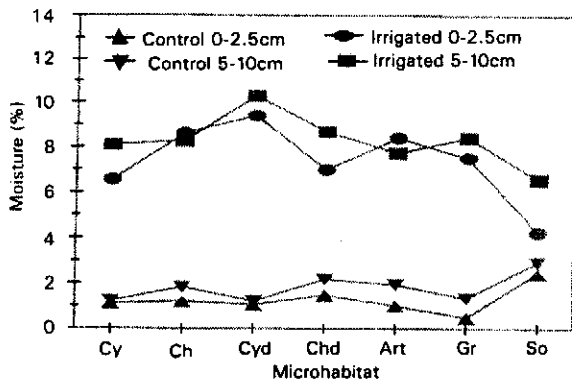


Fig. 3: Percent moisture content at 0-2.5cm and 5-10 depths in natural (control) and above-normal (irrigated) precipitation treatments before spring emergence, April 17, 1997, in seven different microhabitats. Cy = *Cymbopogon jwarancusa* canopy, Ch = *Chrysopogon aucheri* canopy, Cyd = *Cymbopogon jwarancusa* dead center, Chd = *Chrysopogon aucheri* dead center, Art = *Artemisia maritima* canopy, Gr = gravel interspace, So = soil interspace.

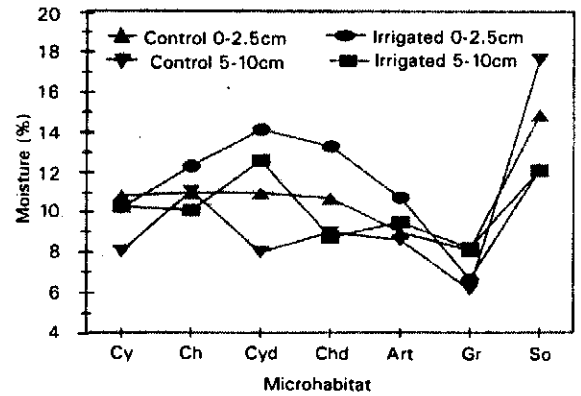


Fig. 4: Percent moisture content at 0-2.5cm and 5-10 cm depths in natural (control) and above-normal (irrigated) precipitation treatments during seedling emergence, May 7, 1997, in seven different microhabitats. Soil moisture content was significantly ($P < 0.05$) higher in soil interspaces than other microhabitats. See Fig. 3 for an explanation of microhabitat abbreviations.

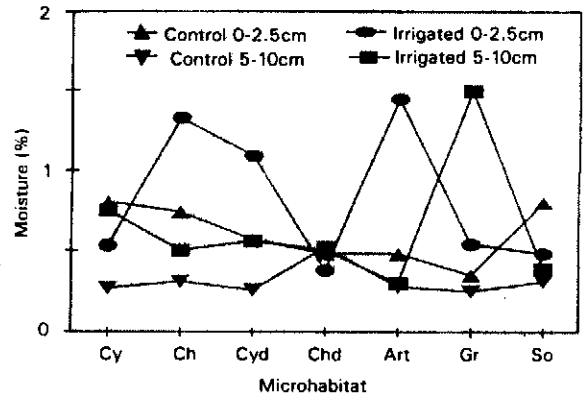


Fig. 5: Percent moisture content at 0-2.5 cm and 5-10 cm depths in natural (control) and above-normal (irrigated) precipitation treatments during the dry season after cessation of supplemental irrigation, Jun 30, 1997, in seven different microhabitats. See Fig. 3 for an explanation of microhabitat abbreviations.

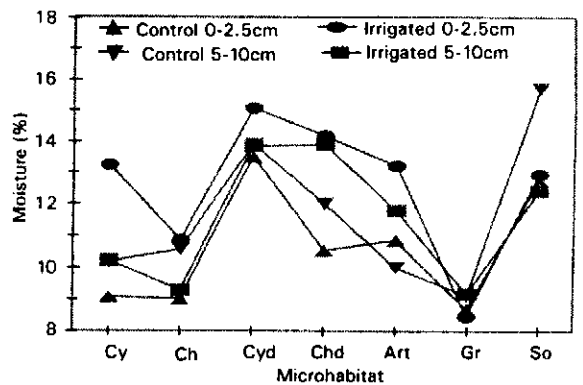


Fig. 6: Percent moisture content at 0-2.5cm and 5-10cm depths in natural (control) and above-normal (irrigated) precipitation treatments during seedling emergence after monsoon rains, July 23, 1997, in seven different different microhabitats. See Fig. 3 for an explanation of microhabitat abbreviations.

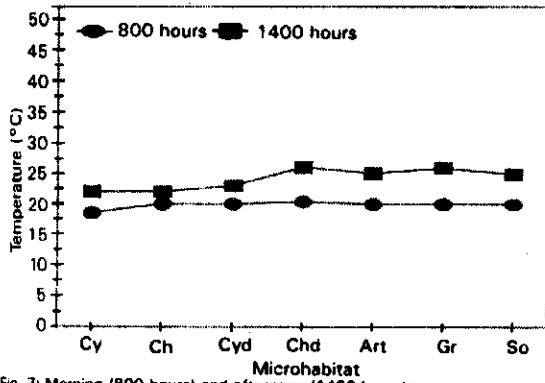


Fig. 7: Morning (800 hours) and afternoon (1400 hours) temperatures before spring seedling emergence, April 17, 1997, in seven different microhabitats (across natural and above-normal precipitation treatments). Soil temperature was significantly ($P < 0.05$) higher in gravel interspaces at 1400 hours than *Cymbopogon jwarancusa* and *chrysopogon aucheri* plant canopies. See Fig. 3 for an explanation of microhabitat abbreviations

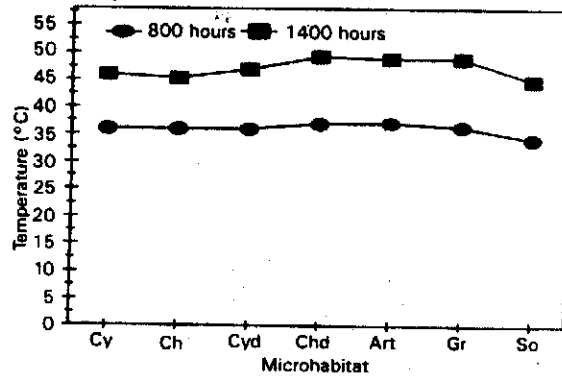


Fig. 10: Morning (800 hours) and afternoon (1400 hours) temperatures during seedling emergence after monsoon rains, July 30, 1997, in seven different microhabitats (across natural and above-normal precipitation treatments). Soil temperature was significantly ($P < 0.05$) higher in gravel interspaces at 1400 hours than *Cymbopogon jwarancusa*, *Chrysopogon aucheri* plant canopies, and soil interspaces. See Fig. 3 for an explanation of microhabitat abbreviations.

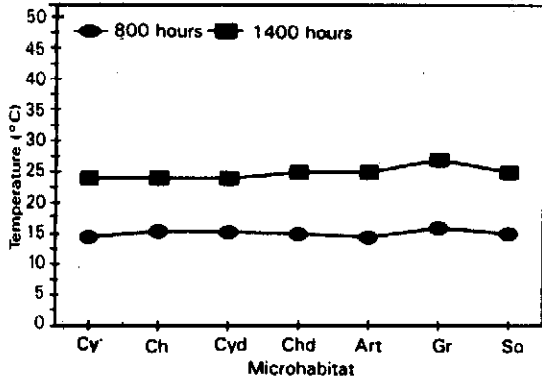


Fig. 8: Morning (800 hours) and afternoon (1400 hours) temperatures during spring seedling emergence, May 7, 1997, in seven different different microhabitats (across natural and above-normal precipitation treatments). Soil temperature was significantly ($P < 0.05$) higher in gravel interspaces at 1400 hours than *Chrysopogon aucheri* and *Artemisia maritima* plant canopies. See Fig. 3 for an explanation of microhabitat abbreviations.

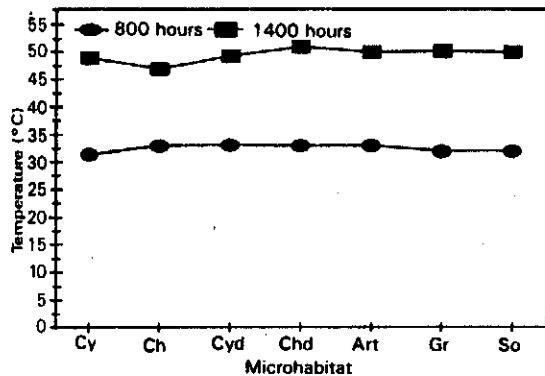


Fig. 9: Morning (800 hours) and afternoon (1400 hours) temperatures during the dry season after cessation of supplemental irrigation, June, 30, 1997, in seven different microhabitats (across natural and above-normal precipitation treatments). Soil temperature was significantly ($P < 0.05$) higher in gravel interspaces at 1400 hours than *Chrysopogon aucheri* plant canopies. See Fig. 3 for an explanation of microhabitat abbreviations.

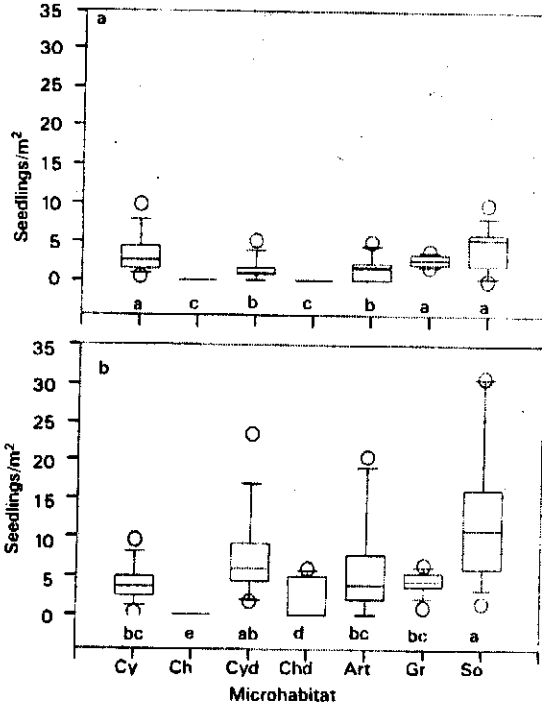


Fig. 11: Box plots showing the densities (seedlings/m²) of emerged seedlings of *Cymbopogon jwarancusa* in (a) the natural precipitation treatment and (b) the above-normal precipitation treatment in May 1997. The horizontal line within the box is the median, the box spans the 25th - 75th percentile range, the verticle lines span the 10th - 90th percentile range, and circles are more extreme values. Microhabitats with different letters are significantly different ($P < 0.05$). See Fig. 3 for an explanation of microhabitat abbreviations.

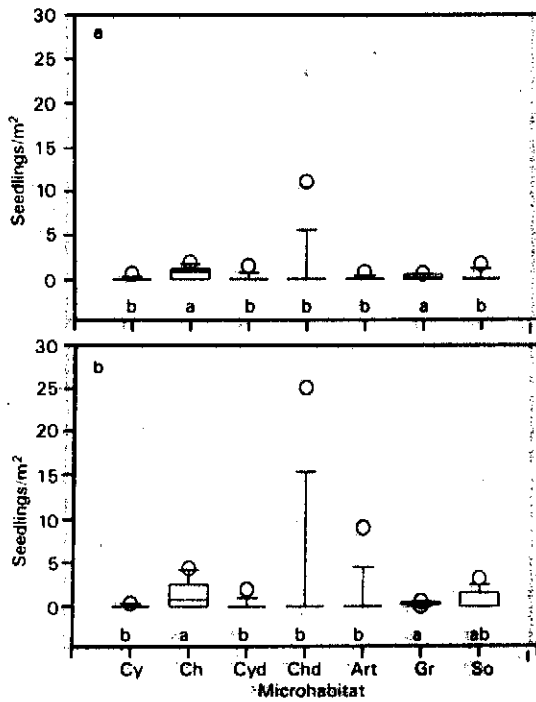


Fig. 12: Box plots showing the densities (seedlings/m²) of emerged seedlings of *Chrysopogon aucheri* in (a) the natural precipitation treatment and (b) the above-normal precipitation treatment in May 1997. Microhabitats with different letters are significantly different ($P < 0.05$). See Fig. 3 and Fig. 11 for an explanation of microhabitat abbreviations and details of box plots.

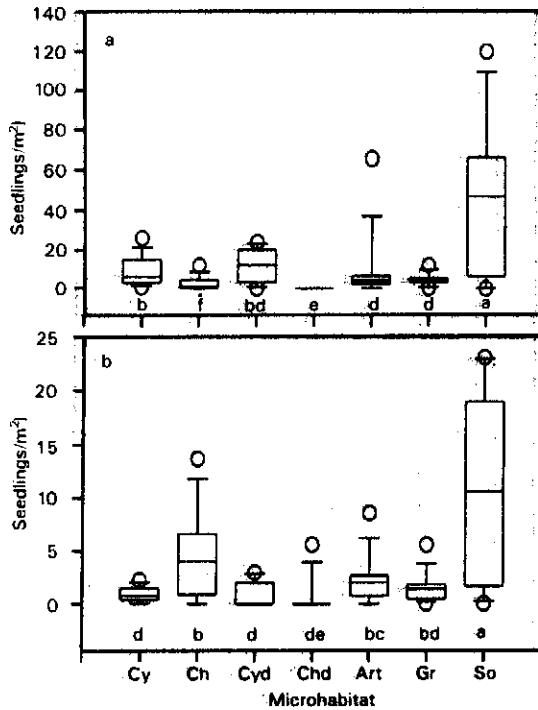


Fig. 13: Box plots showing the densities (seedlings/m²) of emerged seedlings of (a) *Cymbopogon jwarancusa* and (b) *Chrysopogon aucheri* after monsoon rains at the end of July 1997. Y-axis represents different scales for each graph. Microhabitats with different letters are significantly different ($P < 0.05$). See Fig. 3 and Fig. 11 for an explanation of microhabitat abbreviations and details of box plots.

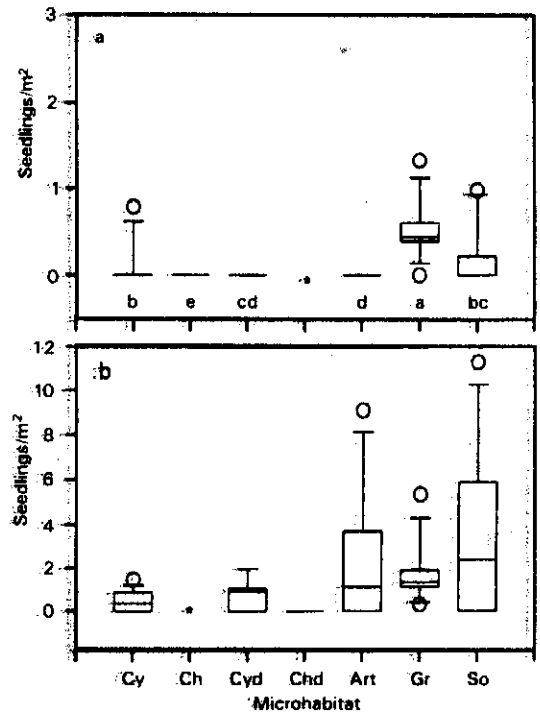


Fig. 14: Box plots showing the densities (seedlings/m²) of survived seedlings of *Cymbopogon jwarancusa* in (a) the natural precipitation treatment and (b) the above-normal precipitation treatment near the end of the growing season in September 1997. Y-axis represents different scales for each graph. * indicates no emergence. Density of survived seedlings was not significantly different among microhabitats in the above-normal precipitation treatment. Microhabitats with different letters are significantly different ($P < 0.05$). See Fig. 3 and Fig. 11 for an explanation of microhabitat abbreviation and details of box plots.

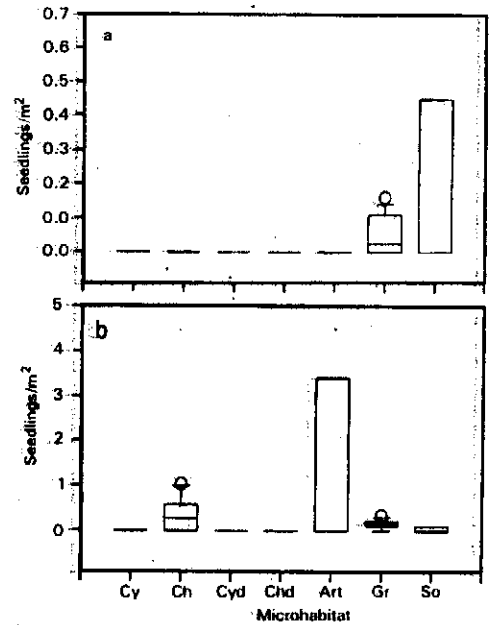


Fig. 15: Box plots showing the densities (seedlings/m²) of survived seedlings of *Chrysopogon aucheri* in (a) the natural precipitation treatment and (b) the above-normal precipitation treatment near the end of the growing season in September 1997. Y-axis represents different scales for each graph. Density of survived seedlings was not significantly different among microhabitats in both natural and above-normal precipitation treatment. See Fig. 3 and Fig. 11 for an explanation of microhabitat abbreviations and details of box plots.

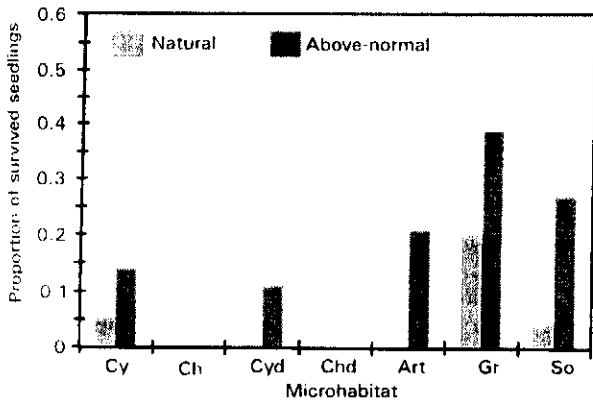


Fig. 16: Proportion of survived *Cymbopogon jwarancusa* seedlings in different microhabitats in natural and above-normal precipitation treatments near the end of the growing season in September 1997. There was no seedling emergence in Chd and Ch in natural and above-normal precipitation treatments, respectively. See Fig. 3 for an explanation of microhabitat abbreviations.

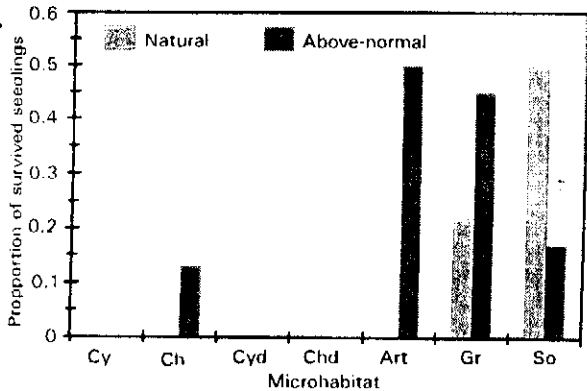


Fig. 17: Proportion of survived *Chrysopogon aucheri* seedlings in different microhabitat in natural and above-normal precipitation treatments near the end of the growing season in September 1997. See Fig. 3 for an explanation of microhabitat abbreviations.

moisture was less than 1.5% in the upper layers (top 10 cm) of all microhabitats until monsoon rains occurred in late July. Gravel surfaces, such as the 2 to 3 cm thick layer observed at the field site, typically act as a mulch, maintaining more favorable moisture levels in the underlying soil than in unprotected soils (Winkel *et al.*, 1991). That was not the case in this study, however.

Diurnal temperature fluctuations varied by only a few degrees in the surface soil layer (top 10 cm) of the microhabitats at each sampling time over the growing season. As noted in other plant communities (Thompson *et al.*, 1977), more open microhabitats (soil and gravel interspaces, and dead centers of both grass species) had slightly higher diurnal fluctuations than microhabitats under plant canopies. During the spring germination and seedling emergence period (late April and early May) for *Chrysopogon aucheri* and *Cymbopogon jwarancusa*, minimum temperatures ranged from 14 to 18 °C and maximum temperatures ranged from 22 to 27 °C across the seven microhabitats. During the monsoon germination and seedling emergence period (late July) for both grass species, minimum temperatures ranged from 32 to 36 °C and maximum temperatures ranged from 45 to 49 °C across the microhabitats. Germination requirements for *Chrysopogon aucheri* and *Cymbopogon jwarancusa* have been investigated in only one

controlled environment study (Saleem, 1990). Saleem (1990) reported that both species had high germination at diurnal air temperatures of 10/30 °C, and maximum germination at 10/20 °C; however, he did not evaluate germination at minimum air temperatures above 10 °C and maximum air temperatures above 30 °C. In one field study, Peart (1984) evaluated the orientation and position of spikelets of 11 grass species, and found that seedlings emerging from vertically oriented spikelets had a better survival rate than seedlings emerging from horizontally oriented spikelets. Rapid radicle penetration into the soil (Peart, 1984) and subsequent development of adventitious roots (Briske and Wilson, 1980) are important for successful seedling establishment in dry environments. Seedlings in gravel interspaces (and soil interspaces) also may have had less competition for water resources than seedlings under canopies and in dead centers of established plants. Surviving seedlings of both grass species under plant canopies did not develop more than one tiller by the end of the growing season. Surviving seedlings of *Cymbopogon jwarancusa* in gravel and soil interspaces developed a maximum of five tillers by the end of the growing season, whereas *Chrysopogon aucheri* seedlings developed only one tiller in all microhabitats.

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