Autecological Characteristics of Chrysopogon aucheri and Cymbopogon jwarancusa, Dominant Rangeland Grasses in Baluchistan

Mohammad Saleem
Utah State University

AUTECOLOGICAL CHARACTERISTICS OF *CHRYSOPOGON AUCHERI* AND *CYMBOPOGON JWARANCUSA*, DOMINANT RANGELAND GRASSES IN BALUCHISTAN

by

Mohammad Saleem

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of

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DEDICATION

To the memory of my father, the late Salim Khan. To my mother, Syeeda-Lo, and my brother, Mohammad Shah, for their love and support, and to my teachers, for their labor and encouragement.

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Mohammad Saleem

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ABSTRACT

Autecological Characteristics of *Chrysopogon aucheri* and *Cymbopogon jwarancusa*, Dominant Rangeland Grasses in Baluchistan

by

Mohammad Saleem, Doctor of Philosophy

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Major Professor: Dr. Christopher A. Call
Department: Range Science

Controlled environment experiments were designed to study the germination, seedling development, and defoliation responses of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* to better understand their autecology and potential use in range improvement programs in Baluchistan.

In experiment 1, *Cymbopogon jwarancusa* had greater seed fill and viability than *Chrysopogon aucheri.* When incubated at six different alternating temperature regimes, seeds of *Cymbopogon jwarancusa* had greater cumulative germination at five temperature regimes and faster germination at the colder temperature regimes than *Chrysopogon aucheri.*

In experiment 2, seedling shoot and root development was characterized at 15-day intervals over a 60-day

period. Seedlings of both species had a "panicoid" type seedling morphology. Chrysopogon aucheri and Cymbopogon jwarancusa developed comparable numbers of leaves and tillers per plant during the 60-day period. Chrysopogon aucheri had a greater number, length, and dry weight of primary and seminal roots than Cymbopogon jwarancusa at 30 and 60 days, respectively. Adventitious root length was also higher for Chrysopogon aucheri than Cymbopogon jwarancusa at 60 days. Seedlings of both species had similar shoot:root ratios and relative growth rates. In experiment 3, seedlings of both species were planted in monocultures and in a 50:50 mixtures. Defoliation treatments, implemented 32 weeks after emergence, included: equally clipping all plants of both species zero, one, two, or three times (at 4-week intervals) in monoculture and mixture; and clipping one species zero, one, two, or three times (at 4-week intervals) without clipping the associated species in mixture. Both species remained vegetative and did not differ in leaf and tiller development until about 32 weeks after emergence. During later growth, Chrysopogon aucheri reproduced while Cymbopogon jwarancusa remained vegetative. Cymbopogon jwarancusa produced more tillers on control plants and defoliated plants (mainly in monoculture). At lower frequencies of defoliation Chrysopogon aucheri produced more shoot and root biomass than Cymbopogon jwarancusa (mainly in mixture). In 50:50 mixtures when one species was defoliated and the other not, both species were comparable in shoot dry weight; however, Chrysopopgon aucheri was superior to Cymbopogon jwarancusa in root dry weight at all defoliation regimes. The initial standing crop and subsequent regrowth of Chrysopogon aucheri were comparable or higher in crude protein and digestibility than Cymbopogon jwarancusa.

(99 pages)

CHAPTER I

INTRODUCTION

Baluchistan, the largest province of Pakistan, has a land area of 347,193 km^2 that comprises 43% of the total area of the country. The climate is arid to semiarid, with annual precipitation ranging from 50 mm in the western part of the province to 450 mm in the northeastern part (Baluchistan Agriculture Department 1985). Maximum and minimum temperatures range from 50 °C in summer to -10 °C in winter. The length of the spring and summer growing season depends upon the pattern and occurrence of precipitation, which can be quite variable (Baluchistan Forest Department 1986). Topographically, the entire province has small mountain ranges and upland valleys with elevations ranging from 1,500 to 2,438 m. Soils are mostly skeletal and are derived from limestone, sandstone, and shale (FAO 1981). Rangeland comprises 94% of the land area of Baluchistan. *Cymbopogon* and *Chrysopogon* grasslands constitute 50 % of the range area of the province (Baluchistan Forest Department 1986).

Historically, *Cymbopogon* and *Chrysopogon* grasslands originated from woodland ecosystems as a result of deforestation, shifting cultivation, and burning (Singh et al. 1985). They are maintained at a subclimax stage

(Clements 1928) by repeated burning and grazing. These grasslands are the major source of forage for local and nomadic herds of livestock (sheep, goats, camels, and cattle) and are grazed continuously either season-long or year-long. Overgrazing has reduced the canopy cover, increased soil erosion potential, and allowed the invasion of undesirable species (Debadgahoa and Shankarnarayan 1973). Rangelands now produce 10 to 50 % less than their potential (Khan 1971), which ranges from less than 30 kg/ha per year to 280 kg/ha per year (FAO 1981).

Chrysopogon aucheri and Cymbopogon jwarancusa, the dominant, perennial, C_4 bunchgrasses on Baluchistan grasslands, have been found growing on a wide variety of soils over a wide range of elevations. Chrysopogon aucheri is readily grazed, whereas Cymbopogon jwarancusa is grazed only after the former has been heavily grazed. The low palatability of Cymbopogon jwarancusa has been related to the oil content in its leaves (West Pakistan Forest Department 1960). As the grasslands deteriorate under heavy grazing pressure, Chrysopogon aucheri is gradually replaced by Cymbopogon jwarancusa, which in turn is gradually replaced by the relatively less palatable shrub, Artemisia maritima.

Objectives

Little is known about the ecology of these grasslands (Khan 1971), and few range improvement programs have been initiated in Baluchistan (Baluchistan Forest Department 1986). To better understand plant requirements for "prudent" grazing, one must understand the morphology, physiology, and long-term competitive abilities of these forage grasses (West 1968, Caldwell 1984). Because these grasses have grown in close association and reproduced under continuous grazing pressure for centuries, one may hypothesize that these two grass species are similar in germination, seedling establishment, defoliation response, and nutritional quality (except for oil content) when grown under similar growing conditions.

Due to a lack of understanding about the autecology of Chrysopogon aucheri and Cymbopogon jwarancusa, studies were designed to investigate their germination, seedling establishment, defoliation response, and nutritional quality. Chapter II examines the germination responses of the two range grasses under different alternating temperature regimes. Chapter III addresses comparative seedling establishment under similar controlled growth conditions. Chapter IV characterizes morphological development, defoliation response, nutritional status, and digestibility of these two bunchgrass species. Chapter V integrates the findings of the experiments and provides suggestions for management applications and future research.

CHAPTER II

ECOLOGY OF CHRYSOPOGON AUCHERI AND CYMBOPOGON JWARANCUSA: GERMINATION RESPONSE

Summary

The ability of Cymbopogon jwarancuas to displace Chrysopogon aucheri on Baluchistan grasslands may be related to recruitment potential in addition to differences in palatability. A controlled environment study was designed to investigate the effects of different temperature regimes on germination responses of these two dominant range grasses. Cumulative germination and rate of germination (mean germination time) were evaluated at six alternating temperature regimes (5/10, 5/15, 5/20, 10/20, 10/25 and 10/30 ^{o}C,12 h night/12 h day) representing possible temperatures in western Baluchistan during the recruitment period (March - May). In addition to having greater seed fill and viability, Cymbopogon jwarancusa had greater and more rapid germination than Chrysopogon aucheri at a wider range of temperatures, especially cooler temperatures.

Introduction

Plant establishment by seedling recruitment, the dominant form of regeneration for most species on rangelands, is only successful when plant requirements for seed germination, seedling development, and subsequent growth are matched with microenvironmental factors of the seedbed (Grubb 1977, Harper 1977). Variation in seed germination between species and between ecotypes of the same species have been attributed to differences in seed development, dormancy mechanisms, seed size, distribution of safe sites and differential responses to temperature, water, light, and gas exchange conditions (Koller 1972, Mayer and Poljakoff-Mayber 1982, Peart 1979, 1984, Fowler 1988).

Limited information is available on the germination requirements of Chrysopogon aucheri and Cymbopogon jwarancusa in Pakistan and of related C_4 species in other regions of the world. Production of viable, germinable seed has been related to inflorescence development in Chrysopogon aucheri (Hussain et al. 1980), and in Cymbopogon jwarancusa, Cymbopogon parkeri, and Cymbopogon oliveri (Ahmed et al. 1978). Ahmed et al. (1978) also observed that Cymbopogon jwarancusa had the highest cumulative germination and most rapid germination rate of the three Cymbopogon species. In Australia, Mott (1978) found that high temperature storage enhanced the germination of Chrysopogon fallax and Chrysopogon latifolius. Rai et al. (1980) observed that older (stored) seed of Chrysopogon fulvus had a higher germination capacity than freshly harvested seed, indicating an afterripening effect. Ghosh and Chatterjee (1981) used several chemical and physical treatments to break the dormancy of seed of Cymbopogon flexuous and Cymbopogon maritime. Primary dormancy was relieved by exposure to continuous light and by treatment with gibberellic acid, kinetin, or potassium nitrate after a period of storage. Secondary dormancy was relived by exposure to low temperature.

The germination studies with Chrysopogon aucheri and Cymbopogon jwarancusa did not simulate the range of temperature and moisture conditions to which seeds of both species are exposed during the germination/recruitment period (March - May) of the growing season in western Baluchistan. The objective of this study was to investigate the effects of different alternating temperature regimes on germination responses of seeds of Chrysopogon aucheri and Cymbopogon jwarancusa collected in the Quetta Region of Baluchistan.

Materials and Methods

Seeds (caryopsis and attached lemma and palea) of Chrysopogon aucheri and Cymbopogon jwarancusa were collected from three protected sites near Quetta, Baluchistan during June and July, 1987. Prior to germination trials in 1988, seeds of both species from the three sites were tested for a caryopsis, and for viability. Five replicates of 100 randomly selected seeds from each site were examined for a caryopsis by removing the lemma and palea. Four replicates of 50 caryopsis from each site were placed in a 1 % triphenyl tetrazolium chloride solution for 24 h at 22 °C in complete darkness to determine viability (Grabe 1970). Percent viability was determined by evaluating intensity of staining and staining patterns under a 10 x lens. Due to low seed fill and viability of Chrysopogon aucheri, seed from the three sites were combined into one lot. Seed of Cymbopogon jwarancusa were also combined into one lot.

In a controlled environment, four replicates of 50 filled seeds of each species were exposed to alternating temperature regimes (12 h night/12 h day, light intensity of 250 μ mol. m^{-2}. sec^{-1} during day period) of 5/10, 5/15, 5/20, 10/20, 10/25, and 10/30 °C, which simulated possible temperature regimes on rangelands near Quetta, Baluchistan from March through May (Table 5 in Appendix). Seeds were placed on two layers of Whatman No.1 filter paper (saturated with distilled water when necessary) in Petri dishes. Petri dishes were wrapped in polyethylene film to reduce evaporation losses and stabilize relative humidity. A seed was considered germinated when it had a radicle greater than 2 mm. Germinated seeds were counted and removed from Petri dishes every day over a 25-day period, and cumulative germination data were reported as a percentage of the total number of filled seeds in each dish. Germination rates were estimated by calculating mean germination time, i.e. the mean time in days taken for nondormant, for viable seeds to germinate (Ellis and Roberts 1978).

The experiment was arranged in a completely randomized design with four replications per treatment for each species. Cumulative germination percentage and mean germination time data were subjected to analysis of variance, and means were separated by Fisher's least significant difference test ($P < 0.05$ level of significance). Cumulative germination percentage data were transformed prior to analysis using an arcsine transformation.

Results

Considerable variability in caryopsis fill, viability, and germination was observed between the two species. Chrysopogon aucheri and Cymbopogon jwarancusa respectively had means of 25 (SD ± 4.4) and 47 % (SD ± 2.3) for seed fill and means of 6 (SD ± 1.6) and 87 % (SD ± 2) for seed viability. Germination did not occur in both species at the coldest temperature regime (5/10 °C) (Table 1). Cymbopogon jwarancusa had limited germination at 5/15 °C while Chrysopogon aucheri did not initiate germination until 5/20 °C. Germination increased with increasing temperature for both species, reaching a maximum value at

Table 1. Cumulative germination (%) of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) seeds as influenced by six alternating temperature regimes. Germination values are not adjusted for seed viability.

Temperature regime (°C)	Germination (%) Ch	Cy
5/10	0.0 a x	0.0 e x
5/15	0.0 a x	12.0 d y
5/20	2.0 a x	63.0 c y
10/20	5.5 a x	86.5 a y
10/25	0.9 a x	65.5 c y
10/30	4.9 a x	74.0 b y

Mean in the same column followed by different letters (a through e) and in the same row followed by different letters (x through y) are significantly different ($LSD_{.05}$ = 7.2).

10/20 °C. Germination for both species declined as temperatures increased from 10/20 to 10/25 °C and then increased as temperatures increased from 10/25 to 10/30 °C. Cymbopogon jwarancusa germination was significantly greater than that of Chrysopogon aucheri at all temperature regimes ranging from 5/15 to 10/30 °C when differences in viability were not considered in the calculation of cumulative germination. However, when the low viability (6%) of Chrysopogon aucheri seeds was considered, cumulative germination was not significantly different between the two species at the optimum temperature range (10/20 °C) and at 10/30 °C (Table 2). Almost all the viable seeds of each species germinated at 10/20 °C.

Mean germination time was significantly slower for both species at colder temperature regimes (5/15 °C for Cymbopogon jwarancusa and 5/20 °C for Chrysopogon aucheri) (Table 3). Mean germination time of Cymbopogon jwarancusa seeds was slightly faster than that of Chrysopogon aucheri seeds at temperature regimes with the greatest cumulative germination (5/20 to 10/30 °C); however, this difference was not significant.

Discussion

Differences in one or several environmental factors (temperature, moisture, light, oxygen, etc.) can result in

Table 2. Cumulative germination (%) of <u>Chrysopogon aucheri</u> (Ch) and <u>Cymbopogon jwarancusa</u> (Cy) seeds as influenced by six alternating temperature regimes. Germination values are adjusted for seed viability.

Temperature regime (°C)	Germination (%) Ch	Cy
5/10	0.0 d x	0.0 e x
5/15	0.0 d x	13.8 d x
5/20	33.3 b x	72.4 c y
10/20	91.6 a x	99.4 a x
10/25	16.6 c x	75.3 c y
10/30	83.3 a x	85.1 b x

Means in the same column followed by different letters (a through e) and in the same row followed by different letters (x through y) are significantly different ($LSD_{.05}$=9.5).

Table 3. Mean germination time (days) of <u>Chrysopogon aucheri</u> (Ch) and <u>Cymbopogon jwarancusa</u> (Cy) as influenced by six alternating temperature regimes.

Temperature regime (°C)	Mean germination time (days)	
	Ch	Cy
5/10	----	---
5/15	---	22.1 a x
5/20	17.6 a x	9.8 b y
10/20	10.3 b x	7.7 b x
10/25	9.0 b x	5.0 b x
10/30	9.1 b x	5.5 b x

Means in the same column followed by different letters (a through b) and in the same row followed by different letters (x through y) are significantly different ($LSD_{.05}$ = 7).

significantly different germination responses of wildland grass species (Ellern and Tadmor 1967, Dwyer and Wolde-Yohannis 1972, Young et al. 1973). Day-night temperature alterations are the normal condition in the field and are required for appreciable germination in many species (Koller 1972). If one temperature is within the upper or lower inhibitory range, the inhibitory effect may be nullified by the other alternating temperature (Gulliver and Hydecker 1973). In the colder temperature regimes, (5/10 to 5/20 °C) the 5 °C low temperature appeared to be inhibitory to the germination of Cymbopogon jwarancusa until the upper temperature reached 15 °C (5/15 °C temperature regime) and to the germination of Chrysopogon aucheri until the upper temperature reached 20 °C (5/20 °C temperature regime) (Tables 1 and 2). Cumulative germination increased significantly for Cymbopogon jwarancusa as the upper temperature reached 20 °C (5/20 °C temperature regime). Thus, considerable germination can occur in cold fluctuating temperature regimes if the soil surface temperature approaches 20 °C during the daytime and moisture is available.

The decline in cumulative germination in the 10/25 and 10/30 °C temperature regimes (Table 1) and the slight increase in mean germination time in the 10/30 °C temperature regime for both species may be attributed to seed variability. The low viability (6%) of filled Chrysopogon aucheri seed made it difficult to consistently place a representative number of viable seeds in Petri dishes for the different germination treatments.

The small amount of literature available on the germination characteristics of Chrysopogon and Cymbopogon species from Pakistan and various range regions supports the findings of this study. Cymbopogon species appear to have higher germinability than Chrysopogon species under a variety of environmental conditions (Mott 1978, Rai et al. 1980, Ghosh and Chatterjee 1981). In one study (Ahmed et al. 1978), Cymbopogon jwarancusa had 99 % germination after 14 days in a 20 - 25 °C temperature regime.

The production of viable, germinable seed by Cymbopogon jwarancusa and Chrysopogon aucheri in Pakistan has been primarily related to inflorescence development. Ahmed et al. (1978) indicated that a relatively high percentage (> 50 %) of sterile florets contributed to low viable seed set (32 % viable seed) in a population of Cymbopogon jwarancusa. Hussain et al. (1980) reported that Chrysopogon aucheri had 60 % sterile florets, and considered this sterility value to be a reliable indicator of poor seed set and germination in this species. In both field nursery studies (Ahmed et al. 1978, Hussain et al.

1980), floret sterility was determined morphologically by quantifying the presence of male, female, bisexual, or barren florets. Female florets were absent in both Chrysopogon aucheri and Cymbopogon jwarancusa; therefore, only bisexual florets were considered capable of seed set. Since nursery growing conditions were relatively more favorable than the field conditions, floret sterility and seed set were probably more influenced by genetic rather than environmental factors.

Seed fill, viability, and germination data from this study generally support the findings of Ahmed et al. (1978) and Hussain et al. (1980). Cymbopogon jwarancusa and Chrysopogon aucheri had 47 and 25 % caryopsis fill, respectively, and filled seeds had 87 and 6 % viability, respectively. It appears that Chrysopogon aucheri has an inherently lower potential for producing viable, germinable seed than Cymbopogon jwarancusa. Based upon seed fill, and viability data, if 1,000 randomly selected seeds of each species were sown under optimum conditions, only 15 Chrysopogon aucheri seeds would have the potential to germinate whereas 409 Cymbopogon jwarancusa seeds could potentially germinate.

The ability of Cymbopogon jwarancusa to displace Chrysopogon aucheri on Baluchistan grasslands has been primarily related to differences in palatability (West Pakistan Forest Department 1960). In addition to being less palatable than Chrysopogon aucheri, it appears that Cymbopogon jwarancusa also has an advantage in recruitment potential. Results demonstrate that Cymbopogon jwarancusa seed not only have higher seed fill, and viability, they also have the capacity for greater germination than Chrysopogon aucheri over a wide range of alternating temperatures (Tables 1 and 3). This may allow Cymbopogon jwarancusa to germinate in a wide variety of seedbed microsites with different temperature regimes when transient soil moisture is available, especially during cooler temperatures in March (Table 5 in Appendix).

CHAPTER III

ECOLOGY OF CHRYSOPOGON AUCHERI AND CYMBOPOGON JWARANCUSA: SEEDLING DEVELOPMENT

Summary

A description of shoot and root morphology is essential for understanding the seedling establishment process in grasses. A controlled environment study, using an 80 % washed sand and 20 % loam soil growing medium, was conducted to determine differences in leaf and tiller development, and primary, subcoleoptile internode, seminal, and adventitious root development between seedlings of Chrysopogon aucheri and Cymbopogon jwarancusa at 15, 30, 45, and 60 days after emergence. In general, seedlings of both species were comparable in terms of shoot and root development over the 60-day growing period. Relative growth rates of total seedling biomass were 0.061 and 0.068 mg. mg^{-1}. day^{-1}, respectively, for Chrysopogon aucheri and Cymbopogon jwarancusa. Both species showed evidence of subcoleoptile internode elongation and subcoleoptile internode root development characteristic of "panicoid" type seedlings.

Introduction

Germination and seedling development are critical stages in the establishment of perennial grasses on arid and semiarid rangelands. Frequently, competitive advantages gained during the seedling stage are maintained in the mature plant stage (Coyne and Bradford 1985). High success in seedling establishment is often associated with rapid root and shoot growth, a robust growth habit, and resistance to environmental stress (McKell 1972). In dry regions, rapid seedling root elongation allows roots to grow along the descending moisture front in subsurface soils (Milthorpe 1950, Harris 1967, Buckly 1982, Simanton and Jordan 1986).

Seedling development and morphology have been used to classify grasses and to provide a basis for understanding the establishment processes in grasses. Hoshikawa (1969) classified 219 species from 88 genera into six seedling types based on root morphology and observed that nearly all species of the same genus were of the same seedling type. More recently, Newman and Moser (1988) described the seedling root morphology of nine cool-season (C_3) and nine warm-season (C_4) perennial forage grasses commonly used in the northern USA. In both studies (Hoshikawa 1969, Newman and Moser 1988), most of the warm-season grasses ("panicoid" seedling type) had an elongated subcoleoptile internode with subcoleoptile internode root development (Fig. 1). The cool-season grasses ("festucoid" seedling type) had little or no subcoleoptile internode elongation and had seminal root development (Fig. 1). Adventitious roots originate at the base of the coleoptile, which is at the depth of seeding for festucoid seedlings and is placed near the soil surface by subcoleoptile internode elongation for panicoid seedlings. Hoshikawa (1969) examined one Cymbopogon species (species unknown) and found it was a panicoid-type seedling.

Dry surface soil prevents the development of adventitious roots, which become the major root system of established plants in many panicoid grasses (Tischler and Voigt 1987). Primary and subcoleoptile internode roots cannot supply sufficient water to keep up with the increasing evaporation demand of the growing shoot (Hyder et al. 1971, Wilson et al. 1976), resulting in seedling mortality and unsuccessful seedlings.

Information is lacking on seedling development and morphology of dominant C_4 forage grasses in Baluchistan. This study was designed to characterize the seedling root and shoot development of Chrysopogon aucheri and Cymbopogon jwarancusa in an effort to better understand their establishment requirements.

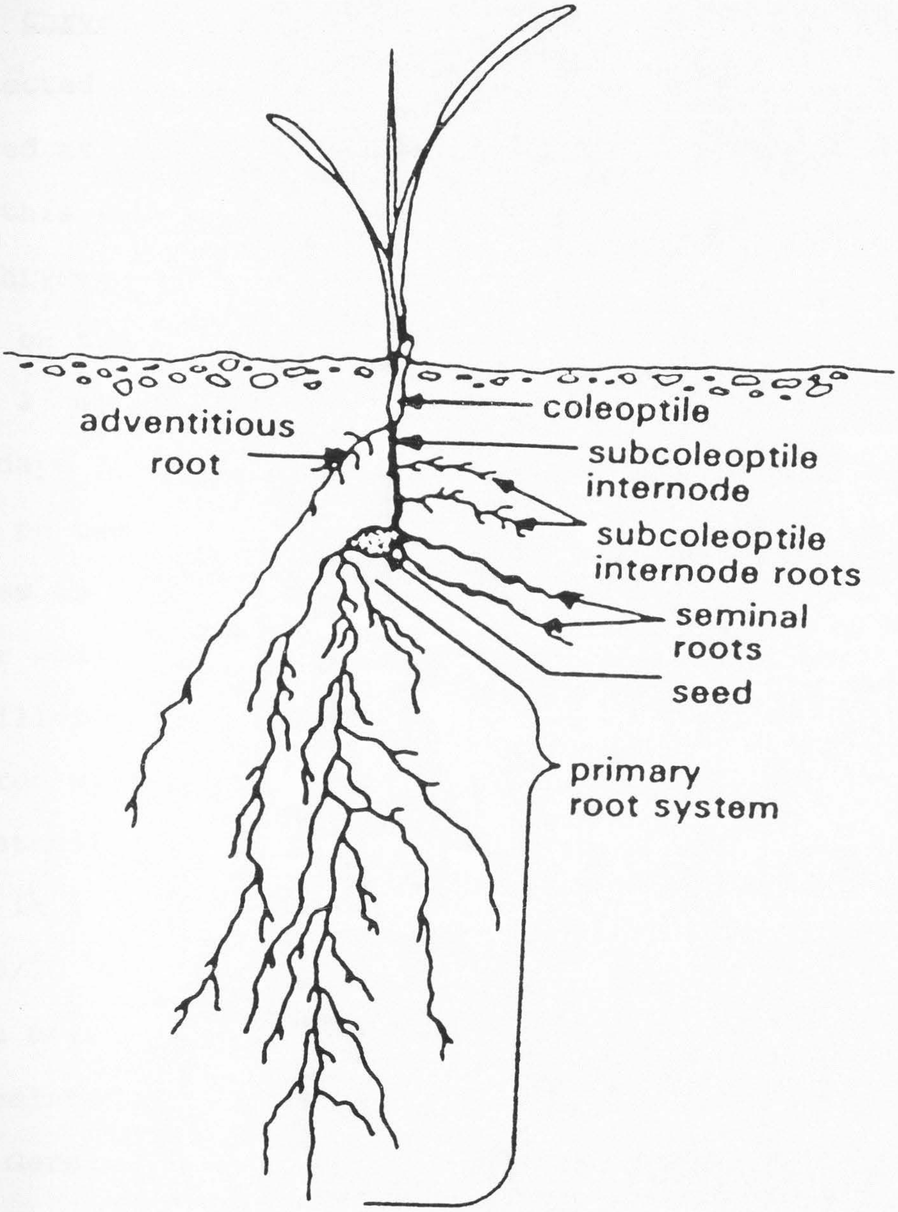


Figure 1. Grass seedling root morphology (from Newman and Moser, 1988).

Materials and Methods

Chrysopogon aucheri and Cymbopogon jwarancusa seeds, collected near Quetta, Baluchistan in summer 1987, were stored at 20 °C and 40 % relative humidity until May, 1989 for this experiment. Due to the low and slow germination of Chrysopogon aucheri, approximately 10,000 seeds were sown on two layers of paper towels in aluminum trays (16 x 33 x 2 cm) to obtain 60 germinated seeds at the same time. Ten days later, 100 seeds of Cymbopogon jwarancusa were sown on two layers of Whatman No. 1 filter paper in Petri dishes to obtain 60 germinated seeds at the same time. Paper media in trays and dishes were saturated with distilled water when necessary, and trays and dishes were covered with polyethylene film to reduce evaporative losses and stabilize relative humidity. Trays and dishes were kept in a growth room with a night/day temperature regime of 20/25 °C and a 12-h photoperiod. A light intensity of 500 μ mol. m^{-2}. sec^{-1} (photosynthetically active radiation) was maintained during the daytime period.

Germinated seeds (radicle approximately 2 mm in length) were transplanted (1.5 cm deep) into pots (6.5 cm diameter, 25 cm deep) filled with 80 % washed sand and 20 % loam soil (v/v), simulating soil conditions in the field near Quetta. The pots were placed in a growth room under the previously described environmental conditions. Maximum and minimum temperatures were recorded daily for the calculation of growing degree days (Wilkins et al. 1984) accumulated after seedling emergence. For the first 15 days after transplanting, pots were watered to field capacity with distilled water every third day. After this 15-day period, pots were watered to field capacity with distilled water or 1/4 strength Hoagland solution (Hoagland and Arnon 1950) on an alternating basis every third day. Seedlings were thinned to one per pot after reaching the second leaf-stage 9 to 10 days after emergence.

Seedlings were destructively harvested at 15, 30, 45, and 60 days after emergence to observe root and shoot development. Seedlings from each pot were carefully washed to remove adhering soil and nearly all roots were retained. Root morphology was assessed according to the root system identification model of Newman and Moser (1988). Root measurements included: primary root number, length, and dry weight; seminal root number, length, and dry weight; and adventitious root number, length, and dry weight. Roots and rootlets exceeding 2 mm in length were counted as separate roots. Root and shoot samples were dried at 60 °C for 48 h to determine dry weights. Seedling shoot development was quantified by recording tiller number and Haun (1973) index every other day throughout the experiment. Tillers were labeled with different color rings, and numbered according to the order of leaves on the main stem. Each new leaf on its first appearance at a growing point was allotted "0" Haun stage and it's subsequent growth was divided into decimal fractions that on each subsequent count accumulated to make one unit when there appeared another leaf. In a similar manner, the growth units were summed to provide the Haun stage per seedling on each harvest date. Seeding shoot development was related to cumulative growing degree days after seedling emergence.

The experiment was arranged in a split plot design with harvest date as the main plot and species as the sub plot. There were 10 replications (pots) for each species at each harvest date. Seedling development data were subjected to repeated measures analysis of variance, and mean comparisons were made using Fisher's least significant difference test (LSD) at the $P < 0.05$ level.

Results

Chrysopogon aucheri and Cymbopogon jwarancusa had similar leaf and tiller development over the 60-day growing period (Figs. 2 and 3). By the last harvest, Chrysopogon aucheri and Cymbopogon jwarancusa had developed 11 leaves and 9 leaves per seedling, respectively. Seedlings of both species had 4 to 5 leaves per tiller.

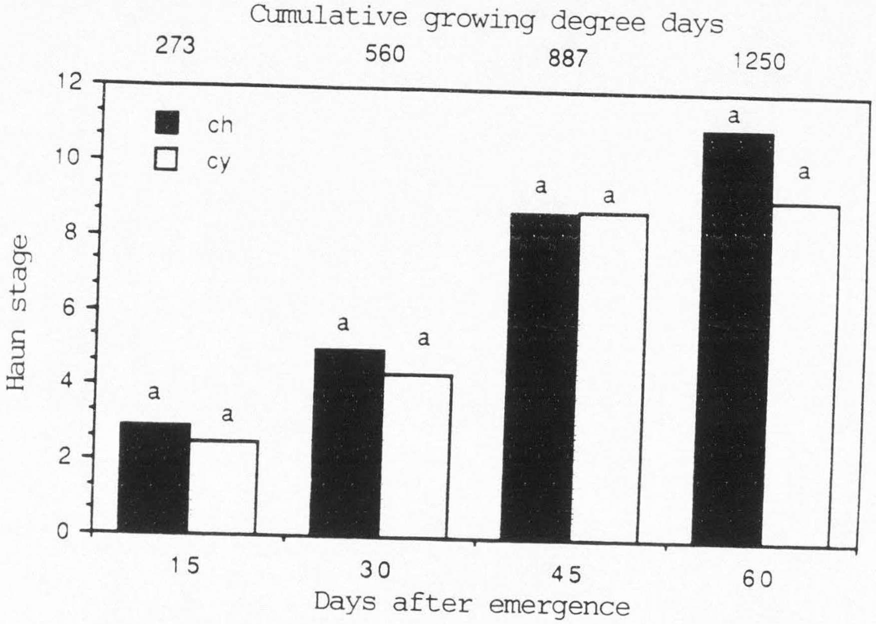


Figure 2. Mean Haun stage (leaf development) of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) seedlings in relation to days after emergence and cumulative growing degree days (CGDD). Values for species at each time interval with different letters are significantly different ($LSD_{.05}$ = 2.45, n = 10).

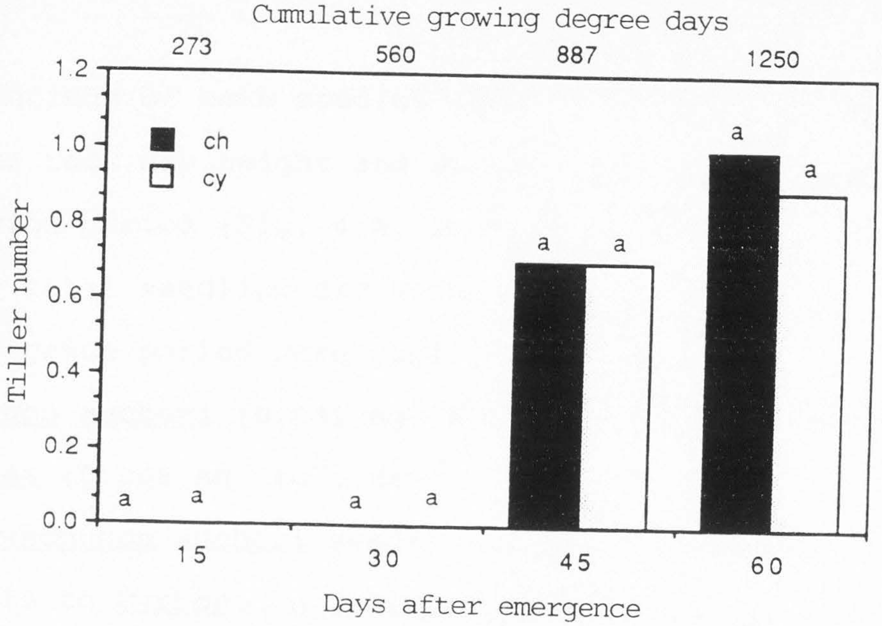


Figure 3. Mean tiller number of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) seedlings in relation to days after emergence and cumulative growing degree days (CGDD). Values for species at each time interval with different letters are significantly different ($LSD_{.05} = 0.87$, n = 10).

Seedlings of both species initiated their first tillers by 45 days after emergence (Fig. 3). By 60 days after emergence, 5 of 10 Chrysopogon aucheri and 3 of 10 Cymbopogon jwarancusa seedlings were initiating a second tiller.

Seedlings of both species were comparable in terms of shoot and root dry weight and shoot:root ratio over the 60-day growing period (Fig. 4 A, B, and C). Relative growth rates of total seedling dry weight for the 15 to 60 day post-emergence period were similar and quite low for Chrysopogon aucheri (0.061 mg. mg^{-1}. day^{-1}) and Cymbopogon jwarancusa (0.068 mg. mg^{-1}. day^{-1}).

Chrysopogon aucheri seedlings were generally comparable to Cymbopogon jwarancusa seedlings in juvenile (primary and seminal roots) and adventitious root development. Seedlings of each species developed 1 main primary root, 1 to 2 main seminal roots, and 5 to 7 main adventitious roots. Total root numbers shown in figures (Figs. 5 A, 6 A, and 7 A) are the sum of the main roots and rootlets (> 2 mm in length) for each root category. By 15 days post-emergence, Chrysopogon aucheri seedlings had a

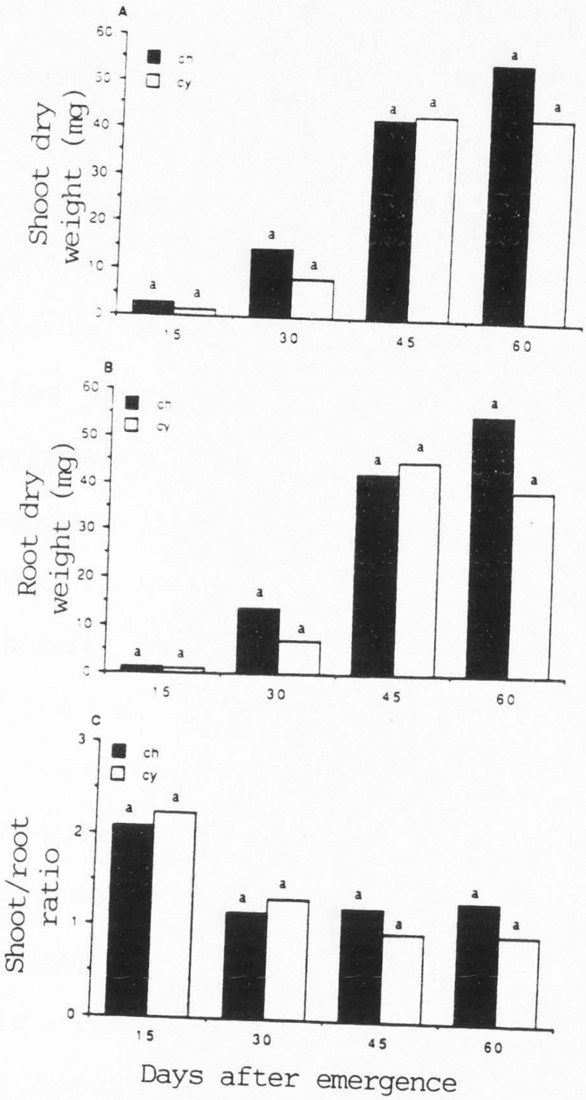


Figure 4. Mean total shoot (A) and root (B) dry weight (mg) and shoot/root ratio (C) of Chrysopogon aucheri (Ch) and Cymbopoton jwarancusa (Cy) in relation to time (days) after emergence. Values for species at each time interval with different letters are significantly different ($LSD_{.05}$ = 23.6 for A, 19.4 for B, and 0.63 for C; n = 10).

significantly greater number and dry weight of primary roots than Cymbopogon jwarancusa seedlings 30 days after emergence (Fig. 5 A, B and C). Differences in primary root development between species lessened over the remaining 30 days of the experiment as seminal and adventitious roots developed. Seedlings of both species initiated seminal roots 15 days after emergence. Seminal roots of Chrysopogon aucheri were greater in number, length and dry weight than Cymbopogon jwarancusa at 60 days post-emergence (Fig. 6 A, B, and C). As with seminal roots, adventitious roots developed slowly over the first 30 days of the experiment (Fig. 7 A, B, and C). Seedlings of both species initiated adventitious roots 15 days after emergence. By 60 days post-emergence, Chrysopogon aucheri seedlings also had significantly greater adventitious root length than Cymbopogon jwarancusa seedlings (Fig. 7 B).

Subcoleoptile elongation was observed on 4 of 10 seedlings of each species at the 15 day harvest interval. Subcoleoptile internodes extended coleoptile nodes 5 to 15 mm above the scutelar node. Only one seedling of each species had 1 to 2 very small (2 mm long) roots on a subcoleoptile internode.

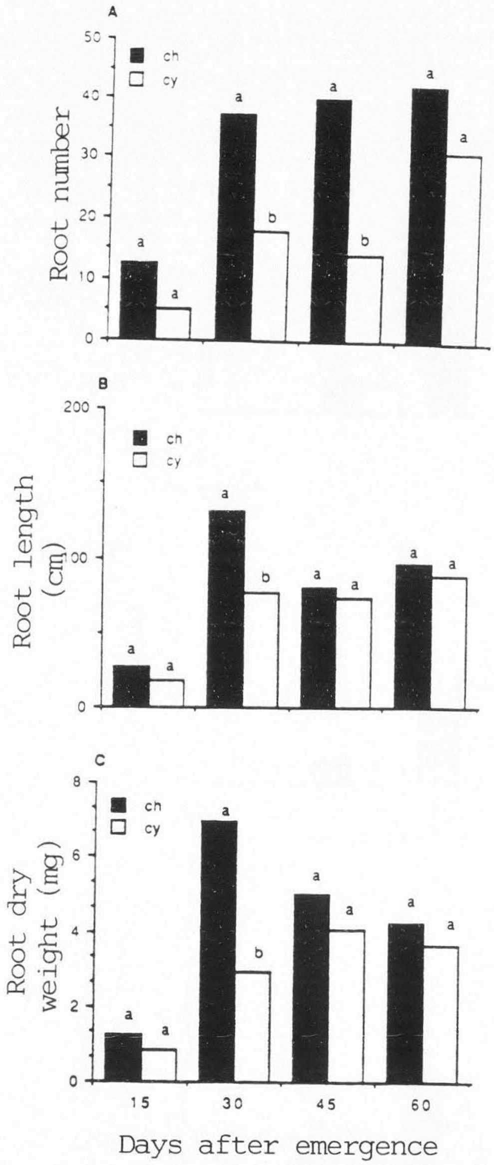


Figure 5. Mean primary root number (main root and rootlets > 2mm) (A), root length (cm) (B), and root dry weight (mg) (C) of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) seedlings in relation to time (days) after emergence. Values for species at each time interval with different letters are significantly different ($LSD_{.05}$ = 15.5 for A, 35.9 for B, and 2.0 for C; n = 10).

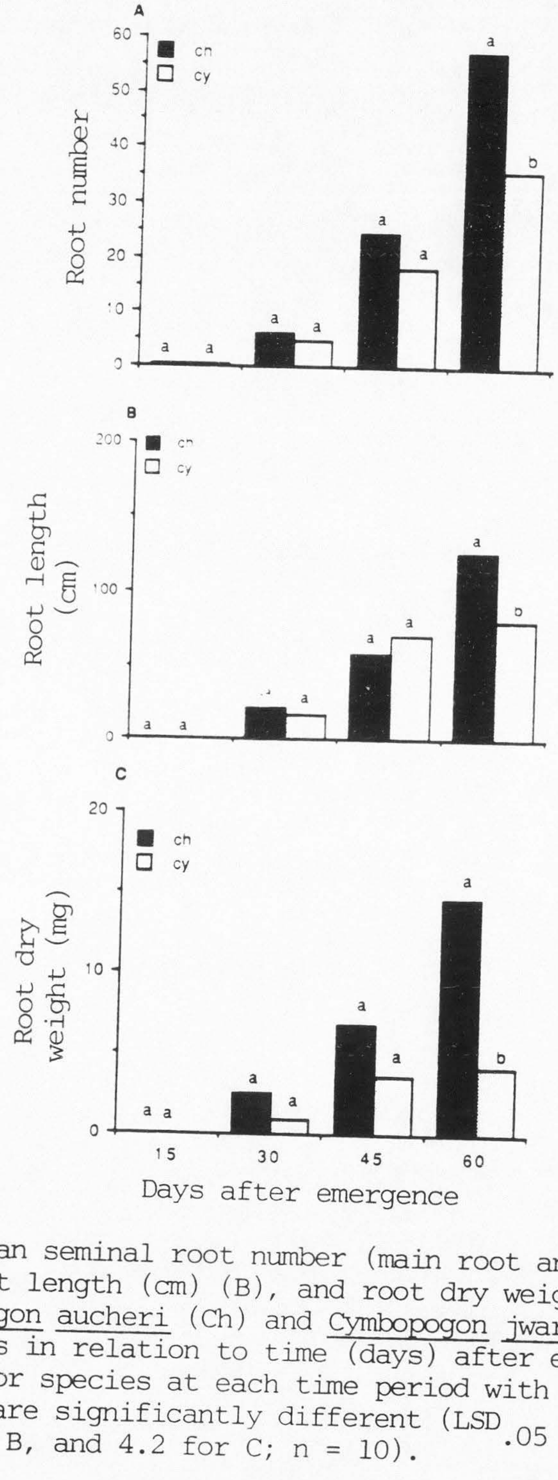


Figure 6. Mean seminal root number (main root and rootlets > 2mm) (A), root length (cm) (B), and root dry weight (mg) (C) of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) seedlings in relation to time (days) after emergence. Values for species at each time period with different letters are significantly different ($LSD_{.05}$ = 22.3 for A, 44.9 for B, and 4.2 for C; n = 10).

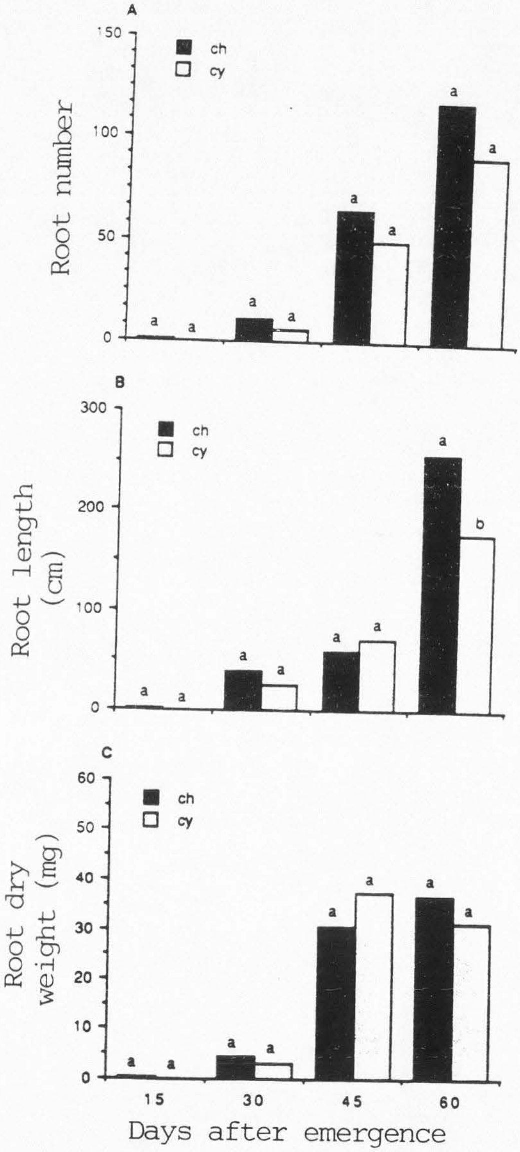


Figure 7. Mean adventitious root number (main root and rootlets > 2 mm) (A), root length (cm) (B), and root dry weight (mg) (C) of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) seedlings in relation to time (days) after emergence. Values for species at each time interval with different letters are significantly different ($LSD_{.05}$ = 45.5 for A, 64.5 for B, and 16.6 for C; n = 10).

When expressed as a proportion (% by weight) of total seedling root dry weight, both species partitioned most resources toward primary root development during the first 30 days of growth and toward adventitious root development 30 to 60 days after emergence (Table 4). Biomass partitioning to the different root types was comparable for both species at all harvest intervals except 60 days after emergence, where Chrysopogon aucheri seedlings had a greater proportion of seminal root biomass than Cymbopogon jwarancusa seedlings.

Discussion

When differences between species occurred, Chrysopogon aucheri seedlings were generally more vigorous than Cymbopogon jwarancusa seedlings under the controlled environmental conditions of this experiment. Seedling vigor in grasses is not characterized by a single attribute, but a combination of attributes such as large seed size, rapid germination, rapid root and shoot growth, tillering ability, and resistance to stress (McKell 1972, Coyne and Bradford 1985). Results from the germination response experiment (Chapter II) demonstrated that Cymbopogon jwarancusa seeds had greater cumulative germination and a more rapid rate of germination than Chrysopogon aucheri seeds. However, Chrysopogon aucheri

Table 4. Mean proportion (% by weight ± SD) of different root types at different stages of seedling development for Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy).

Species and root type	Days after emergence			
	15	30	45	60
Ch	%			
primary	83 ± 31	51 ± 8.8	19 ± 16.8	8 ± 6.9
subcoleoptile internode	T*	0	0	0
seminal	T	17 ± 13	19 ± 13.2	29 ± 8.6
adventitious	17 ± 31	32 ± 9.3	62 ± 15.2	63 ± 9.4
	100	100	100	100
Cy				
primary	98 ± 7.6	47 ± 15	14 ± 10.4	10 ± 3.6
subcoleoptile internode	T	0	0	0
seminal	T	11 ± 10	11 ± 7.3	12 ± 4.5
adventitious	2 ± 7.6	42 ± 11.3	75 ± 16.3	78 ± 7.0
	100	100	100	100

* T = trace amount of biomass too small to contribute to overall root biomass.

seeds contained larger caryopses (4.5 ± .4 mm long, 0. 97 ± .04 mg mass) than those of Cymbopogon jwarancusa (1.6 ± .3 mm long, 0.47 ± .03 mg mass) indicating that Chrysopogon aucheri seedlings may have the potential to emerge from greater soil depths and have greater resources for initial seedling growth (McKell 1972, Fenner 1983). Once germinated, Chrysopogon aucheri seedlings were comparable to Cymbopogon jwarancusa seedlings in all the measured shoot and root parameters. However, at 30 and 60 days post-emergence, primary and seminal root number, length, and dry weight were respectively significantly greater for Chrysopogon aucheri seedlings, as was adventitious root length at 60 days post-emergence. Rapid root elongation is a key characteristic for successful establishment in arid and semiarid areas where surface soils can dry quickly after a precipitation event (McKell 1972, Plummer 1943).

High relative growth rates (increase in terms of biomass invested) and low shoot:root ratios are generally considered to be important survival and environmental adaptations of seedlings (McKell 1972). In this study, both Chrysopogon aucheri and Cymbopogon jwarancusa seedlings had comparably low relative growth rates and initially high shoot:root ratios, indicating that establishment problems could arise in stressful environments. However, Coyne and Bradford (1985) observed that high relative growth rates were not necessarily desirable traits for the establishment of 17 C_4 perennial grasses grown under limiting watering regimes in a controlled environment. Species with highest growth efficiencies at the start of sampling were the ones which had the greatest decline in efficiency by the end of the 51-day growing period. The mean relative growth rate of total seedling biomass for the 17 grasses was 0.133 g. g^{-1}. day^{-1}. Simanton and Jordan (1986) reported that seedlings of Bouteloua curtipendula, a C_4 grass, had low shoot:root ratios, rapid germination, and rapid root elongation, yet had poor establishment in areas of the Southwestern U.S. with less than 190 mm summer rainfall and when subsurface soil moisture is low. In contrast, Eragrostis lehmanniana X Eragrostis trichophora, another C_4 grass with higher shoot:root ratios, slower germination rates, and slower seminal root elongation had more successful establishment on similar semiarid rangelands.

Even though leaf development was not significantly different for seedlings of both species, Chrysopogon aucheri seedlings reached the third leaf stage about 15 days after emergence, whereas Cymbopogon jwarancusa reached the third leaf stage about 18 days after emergence. Newman and Moser (1988) reported that seedlings of several warm-season (C_4) grasses, including Bouteloua curtipendula, B. gracilis, Eragrostis tricodes, Andropogon gerardii var.

gerardii, Schizachyrium scoprium, Bothriochola caucasia, and Panicum virgatum, reached the third leaf stage 15 to 24 days after emergence in a controlled environment study, and that members of the Andropogoneae tribe reached the third leaf stage 3 to 8 days earlier than other warm-season grass species. Chrysopogon aucheri and Cymbopogon jwarancusa, both members of the Andropogoneae tribe, followed a similar pattern of leaf development, in terms of reaching the third leaf stage when adventitious root development typically occurs (Newman and Moser 1988). Rapid leaf and tiller development have also been associated with greater length, number, and order of branching of juvenile (primary and secondary roots) and adventitious roots in seedlings of Bouteloua curtipendula (Wilson and Briske 1979) and Bromus tectorum (Aguirre 1989). The sooner seedling roots increase their depth and volume of soil penetration, the greater is the probability of successful establishment in arid and semiarid regions as moisture becomes limiting in upper soil layers (Plummer 1943, Cook 1980, Buckly 1982, Aguirre 1989).

Successful establishment of grass seedlings requires formation of adventitious roots. The primary root, under normal conditions, is a short-lived structure (Tischler and Voigt 1987), and seminal roots and the subcoleoptile internode do not have sufficient xylem diameters to support water transport to maturing seedlings (Hyder et al. 1971, Wilson et al. 1976). Subcoleoptile internode roots probably contribute less to the water economy of the shoot than primary or seminal roots (Tischler and Voigt 1987). Under the favorable environmental conditions of this study, adventitious roots initiated on seedlings of both species by 15 days after emergence, and comprised the greatest proportion of root biomass by 45 days after emergence. As with other C_4 grasses with panicoid type seedlings, the subcoleoptile internode of Chrysopogon aucheri and Cymbopogon jwarancusa seedlings usually elevates the coleoptile to the soil surface, and adventitious roots typically develop close to the soil surface (Tischler and Voigt 1987). This type of morphology can be detrimental to seedling establishment in regions with limited precipitation, because adventitious roots may develop in the harsh environment associated with the soil surface, and primary and seminal roots cannot meet the water requirements of seedling leaves (Hyder et al. 1971).

Results from this controlled environment study may vary considerably from results obtained under field conditions. Temperature, moisture, and nutrient conditions were considerably more favorable in the laboratory than in the field near Quetta, and most importantly, seedlings of the more palatable Chrysopogon aucheri were not subjected to defoliation. Seedlings of both species have been observed at protected sites near Quetta and other regions of Baluchistan (Saleem, personal observation). Cymbopogon jwarancusa may have a greater potential for germination than Chrysopogon aucheri, but once germination has occurred the fewer Chrysopogon aucheri seedlings may have equal or greater vigor and establishment success on areas protected from grazing.

CHAPTER IV

ECOLOGY OF CHRYSOPOGON AUCHERI AND CYMBOPOGON JWARANCUSA: MORPHOLOGY AND DEFOLIATION RESPONSE

Summary

Little is known about the defoliation responses of the palatable grass *Chrysopogon aucheri*, and the co-occurring unpalatable grass, *Cymbopogon jwarancusa*, under managed and unmanaged conditions on Baluchistan rangelands. Both species were grown in monoculture and in a 50:50 mixture in an 11-month (44-week) greenhouse study. Defoliation treatments were implemented when plants were 32 weeks old; and consisted of: equally clipping (3-cm stubble height) plants in monoculture and mixture zero, one, two, or three times at 4-week intervals (32, 36, and 40 weeks after emergence), and clipping (3-cm stubble height) one species in mixture zero, one, two, or three times at 4-week intervals (32, 36, and 40 weeks after emergence) without clipping the associate species. The final harvest of all plants in every defoliation treatment occurred at 44 weeks after emergence. Response to defoliation was measured in terms of leaf and tiller development, shoot and root biomass production, and nutritional quality and digestibility. Plants of both species had similar patterns of leaf and tiller development until defoliation treatments

were implemented. *Cymbopogon jwarancusa* produced more tillers per plant than *Chrysopogon aucheri* when both species were equally defoliated one, two, or three times in monoculture and equally defoliated three times in mixture. Most *Chrysopogon aucheri* plants developed inflorescences by 32 weeks after emergence, whereas all *Cymbopogon jwarancusa* plants remained vegetative throughout the experiment. *Chrysopogon aucheri* had greater shoot and root biomass than *Cymbopogon jwarancusa* in mixture when plants were equally defoliated zero, one, or two times, whereas shoot and root biomass were comparable under the same defoliation regimes in monoculture, and when equally defoliated three times in monoculture or mixture. When one species was defoliated zero, 1, 2 or 3 times and the associated species was not defoliated, shoot biomass was comparable for both species while *Chrysopogon aucheri* had greater root biomass than *Cymbopogon jwarancusa*. *Chrysopogon aucheri* had similar or higher crude protein content and % in vitro digestible dry matter when compared to *Cymbopogon jwarancusa*. *Chrysopogon aucheri* may not decrease in mixed *Chrysopogon* - *Cymbopogon* communities if the frequency and intensity of defoliation are controlled more closely as in this experiment.

Introduction

Several factors, including the morphology, physiology, and palatability of plants, the type of herbivore, the intensity, frequency, and timing of defoliation, and competition from surrounding plants, can differentially shape the defoliation responses of plants (Menke and Trilica 1981, Archer and Tieszen 1986, Wangoi and Hansen 1987). High rates of refoliation and tillering, high shoot:root and vegetative:reproductive ratios, and late elevation of apical meristems are associated with increased grazing tolerance (Dahl and Hyder 1977, Richards 1984, Archer and Tieszen 1986, Briske 1986). Milthorpe and Davidson (1966) reported that regrowth following defoliation in many grasses was first limited by carbohydrate reserves, then by photosynthesis, and later on by nutrient uptake. However, more recently, Richards and Caldwell (1985) demonstrated that regrowth in two Agropyron bunchgrass species was most influenced by meristematic activity and photosynthesis and not by stored carbohydrate reserves. Plant and shard physical and chemical characteristics, such as growth stage, leaf:stem ratio, availability and distribution of plant parts, and nutrient and fiber content, influence the palatability of forage plant (Holm and Elloit 1980, Minson 1982, Hodgson 1982). These factors influence the bite size, intake, and digestibility of forage (Hodgson 1982). Plant secondary compounds, including essential oils, can greatly reduce palatability. Even though considered a nutritious forage, Cymbopogon jwarancusa is not readily grazed because of a high essential oil content, comprised primarily of piperidine (Chopra et al. 1956, Saeed et al. 1978).

In Baluchistan, *Chrysopogon* - *Cymbopogon* grasslands are grazed continuously by a variety of herbivores, including cattle, and mixed herds of sheep, goats, horses, and camels. These herbivores vary in their grazing behavior and plant preference (Wangoi and Hansen 1987), which makes it difficult to speculate about patterns of defoliation. However, the continuous use of this scarce vegetation resource results in intensive, frequent defoliation of available forage species throughout time during the growing season.

Plant response to defoliation varies considerably with the level of competition from surrounding plants (Mueggler 1972). Highly preferred plants like *Chrysopogon aucheri* are often more frequently and intensively defoliated than less palatable species such as *Cymbopogon jwarancusa* and *Artemisia maritima.* Over time, reductions in above- and below-ground biomass of *Chrysopogon aucheri* may allow the encroachment of associated, less palatable species. Little is known about the growth and development and defoliation responses of *Chrysopogon aucheri* and *Cymbopogon jwarancusa* in a competitive environment. This study was designed to investigate the morphological characteristics of both species, and their responses to different defoliation regimes in a competitive environment.

Materials and Methods

This experiment was conducted in a greenhouse under natural light conditions in Logan, Utah from November 1988 to August 1989. Temperatures ranged from 11 to 23 °C in winter months and 13 to 34 °C in summer months. Two-month-old seedlings of each species were transplanted (November 1988) into pots (28 cm diameter X 36 cm height) in monoculture and in a 50:50 mixture. Monocultures had 4 plants per pot and mixtures had 2 plants per species (arranged alternate to each other) per pot, giving a density equivalent to 15 plants/m^2. The soil medium, composed of 80 % washed sand and 20 % loam soil, simulated the dominant soil texture on rangelands in Baluchistan. Pots were maintained at 50 % of field capacity (determined by pressure plate analysis) throughout the study. Plants were alternately watered (every 3-5 days) with distilled water and 1/4 - strength Hoagland solution (Hoagland and Arnon 1950).

Defoliation treatments, implemented when plants were 32 weeks old, consisted of: equally clipping all plants in monoculture and mixture for zero, one, two, or three times at 4-week intervals (32, 36, and 40 weeks after emergence); and clipping one species in mixture zero, one, two, or three times at 4-week intervals (32, 36, and 40 weeks after emergence) without clipping the associated species in the same pot (Fig. 8). The final harvest of all plants in every defoliation treatment occurred at 44 weeks after emergence. Defoliation treatments were based upon field observations where Chrysopogon aucheri plants are intensively defoliated several times before Cymbopogon jwarancusa plants are defoliated. Plants were clipped to a 3-cm stubble height at each clipping interval. This stubble height simulated a heavy intensity of defoliation (85 % removal of initial standing crop).

Control plants (0 clipping) were monitored for leaf and tiller development at 4-week intervals from week 12 to week 44 (end of experiment). Leaf development of the main stem and subsequent tillers was determined by using the technique of Haun (1973). Each new leaf was identified with a permanent color mark and each new tiller was marked by a different colored ring at its base. Total plant Haun stage was obtained by summing the Haun stage of the main stem and the other tillers as they appeared over time. Prior to the initial clipping at 32 weeks, all live and dead tillers were counted on all plants in monoculture and mixture. After the initial clipping, the main stem and a secondary and tertiary tiller on each plant were marked and monitored for survival and leaf development for the remainder of the experiment.

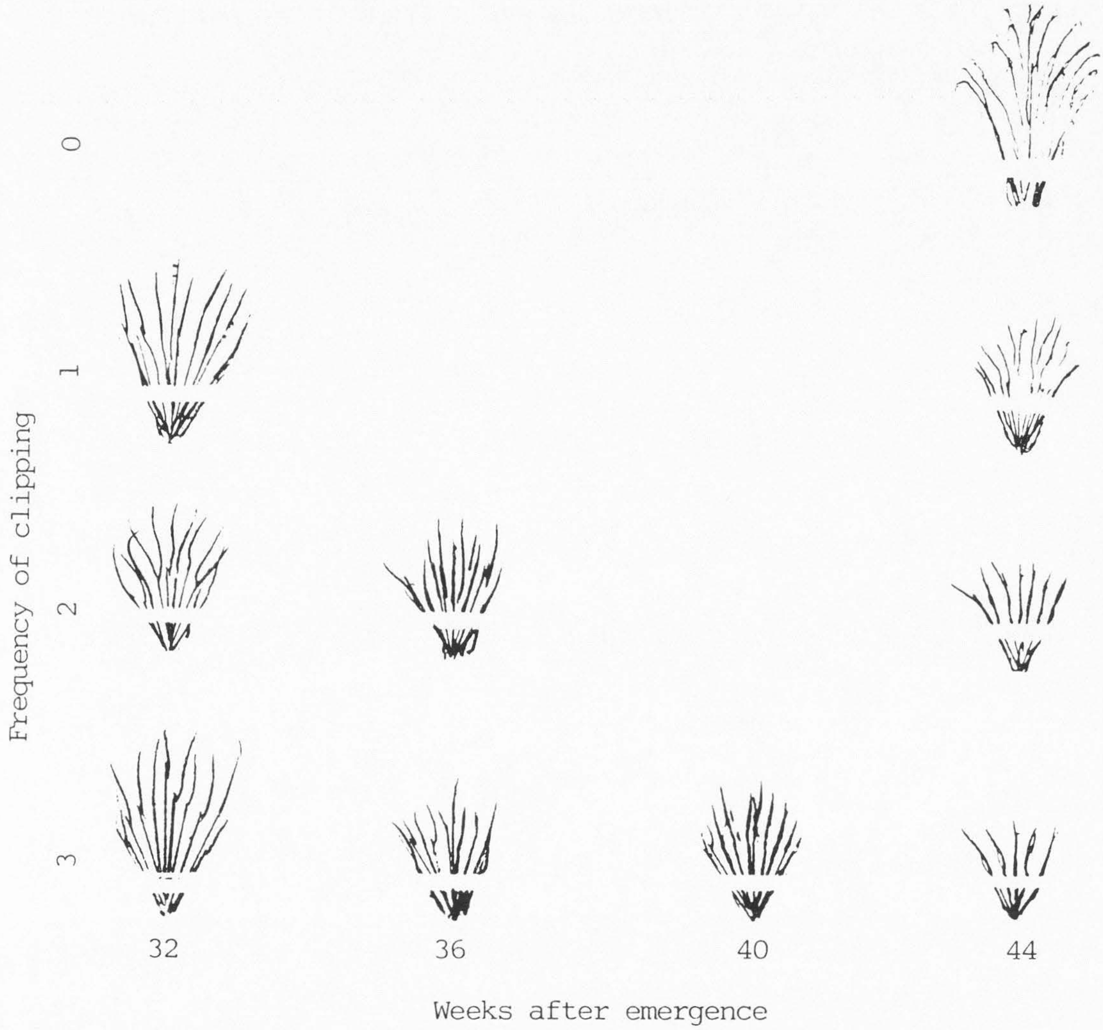


Figure 8. Defoliation treatments for Chrysopogon aucheri and Cymbopogon jwarancusa grown in monoculture and mixture. 0 clip (control) = standing crop clipped at 44 weeks (final harvest) after emergence; 1 clip = standing crop clipped at 32 weeks and regrowth clipped at 44 weeks after emergence; 2 clip = standing crop clipped at 32 weeks and regrowth clipped at 36 and 44 weeks after emergence; and 3 clip = standing crop clipped at 32 weeks and regrowth clipped at 36, 40, and 44 weeks after emergence.

Shoot biomass was determined at appropriate clipping intervals for defoliated plants, and shoot and root biomass were determined at the end of the experiment for defoliated and control plants. Shoot and root biomass samples were oven dried at 65 °C for 48 h prior to weighing. Roots of the two species were intermingled in the mixture pots, but were relatively easy to separate because roots of Chrysopogon aucheri are dark brown while roots of Cymbopogon jwarancusa are pale yellow. Shoot samples from the monoculture treatments were analyzed for % dry matter, % organic matter (Harris 1970), % in vitro digestible dry matter (Goto and Minson 1977), and % crude protein (Hatch et al. 1985).

The experiment was a factorial with 2 species and 20 clipping treatments with four replications (pots) per clipping treatment (see Table 6 in Appendix). Data were subjected to analysis of variance and treatment means were separated by Fisher's least significant difference test (LSD) at the $P < 0.05$ level of significance.

Results

Without defoliation, both species had a similar pattern of leaf and tiller development in monoculture or mixture from 12 to 28 weeks after emergence (Figs. 9 and 10). Cymbopogon jwarancusa produced more tillers per plant

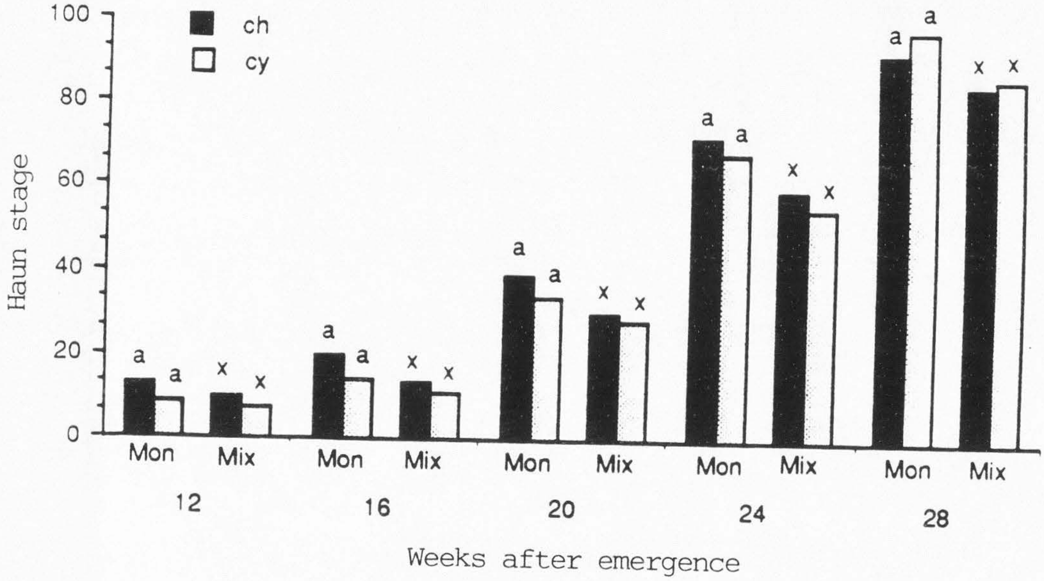


Figure 9. Mean whole plant Haun stage for Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in monoculture (Mon) and mixture (Mix) without clipping. Values for species with different letters within monoculture or mixture at each time interval are significantly different ($LSD_{.05}$ = 14.4; n = 8).

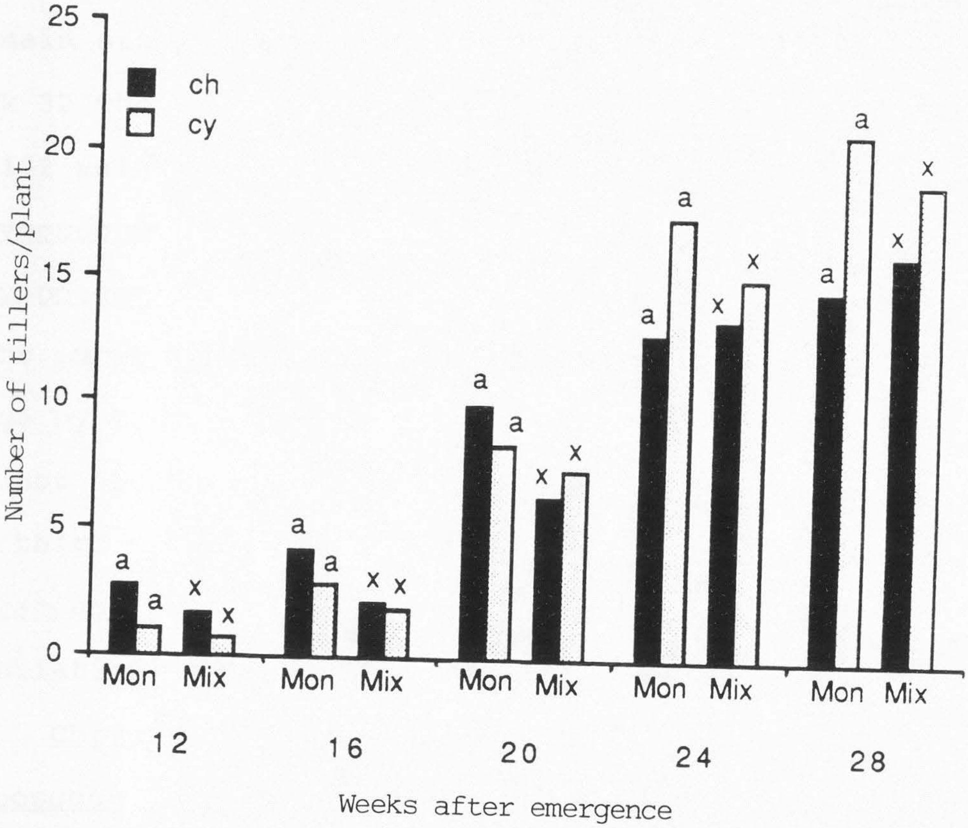


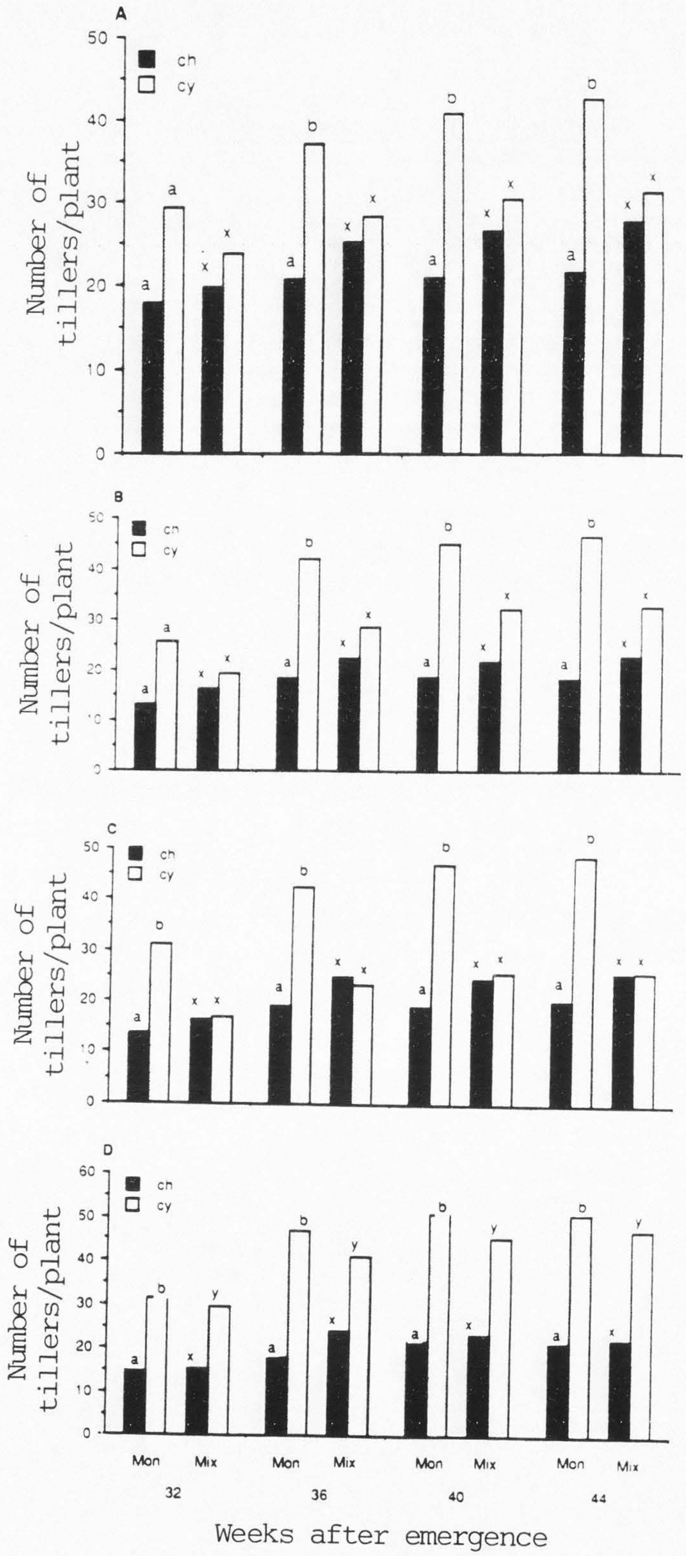
Figure 10. Mean number of tillers per plant for Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in monoculture (Mon) and mixture (Mix) without clipping. Values for species with different letters within monoculture or mixture at each time interval are significantly different ($LSD_{.05}$ = 5.8; n = 8).

than Chrysopogon aucheri at all sampling dates after 36 weeks when both species were equally defoliated zero, one, two, or three times in monoculture (Fig. 11 A, B, C and D), and at all sampling dates when both species were equally defoliated three times in the mixture (Fig. 11 D).

Chrysopogon aucheri plants elongated apical meristems on main stems as early as 24 weeks after emergence. By week 32 when defoliation treatments were implemented, 144 of 192 main stems and 307 of 3075 secondary tillers on Chrysopogon aucheri plants had developed inflorescences. Chrysopogon aucheri plants defoliated one time (32 weeks after emergence) in monoculture or mixture entered the boot stage by the second clipping (36 weeks after emergence) but did not show signs of floral development after the second and third clippings (40 weeks after emergence). Cymbopogon jwarancusa plants remained vegetative regardless of the defoliation regime.

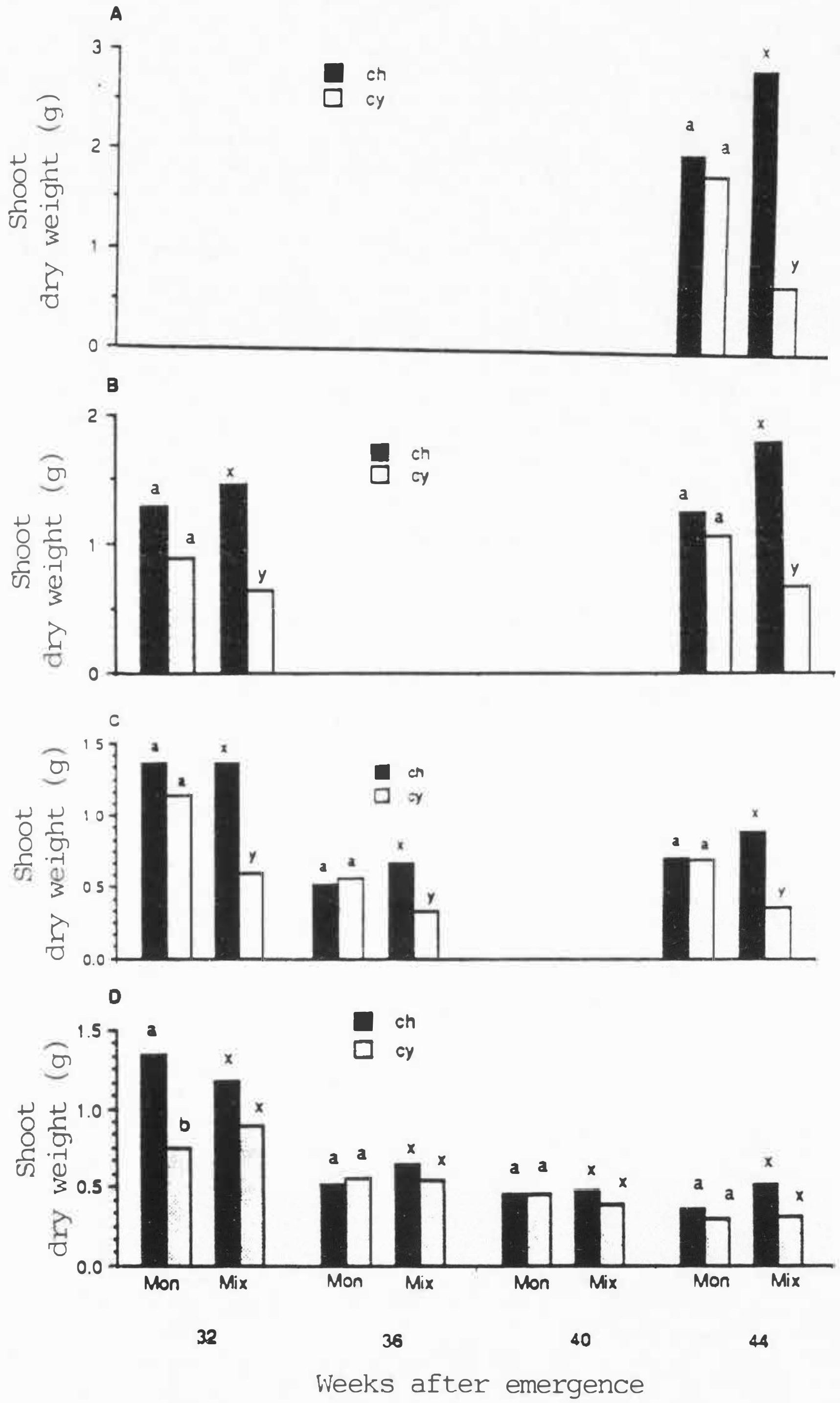
Chrysopogon aucheri had more shoot dry weight than Cymbopogon jwarancusa in mixture when plants were equally defoliated zero, one, or two times (Fig. 12 A, B, and C). Shoot dry weight was comparable for both species in monoculture under the same defoliation regimes (except for week 32 of the 3 clip treatment) and in mixture when plants were equally defoliated three times (Fig. 12 A, B, C, and D). Cumulative shoot dry weight (sum of initial standing crop and regrowth above 3-cm stubble height)

Figure 11. Mean number of tillers per plant for *Chrysopogon aucheri* (Ch) and *Cymbopogon jwarancusa* (Cy) plants grown in monoculture (Mon) and mixture (Mix) under different clipping regimes (3-cm stubble height): (A) 0 clip (control); (B) 1 clip = standing crop clipped at 32 weeks and regrowth at 44 weeks (final harvest) after emergence; (C) 2 clip = standing crop clipped at 32 weeks and regrowth clipped at 36 and 44 weeks after emergence; (D) 3 clip = standing crop clipped at 32 weeks and regrowth clipped at 36, 40, and 44 weeks after emergence. Values for species with different letters within monoculture or mixture at each time interval are significantly different [$LSD_{.05}$ (A, B, C, and D) = 10.1 for 32 weeks, 12.0 for 36 weeks, and 12.8 for 40 and 44 weeks; n = 4].



A
B
C
D
ch
cy
Number of tillers/plant
Mon
Mix
32
36
40
44
Weeks after emergence

Figure 12. Mean shoot dry weight (g) of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in monoculture (Mon) and mixture (Mix) under different clipping regimes (3-cm stubble height): (A) 0 clip (control) = standing crop clipped at 44 weeks (final harvest) after emergence; (B) 1 clip = standing crop clipped at 32 weeks and regrowth clipped at 44 weeks after emergence; (C) 2 clip = standing crop clipped at 32 weeks and regrowth clipped at 36 and 44 weeks after emergence; (D) 3 clip = standing crop clipped at 32 weeks and regrowth clipped at 36, 40, and 44 weeks after emergence. Values for species with different letters within monoculture or mixture at each time interval are significantly different [$LSD_{.05}$ (A, B, C, and D) = 0.61 for 32 weeks, 0.36 for 36 weeks, 0.22 for 40 weeks, and 0.35 for 44 weeks; n = 4].


A
B
C
D
ch
cy
Shoot dry weight (g)
Mon
Mix
32
36
40
44
Weeks after emergence

(Fig. 13), crown dry weight (below 3-cm stubble height) (Fig. 13), and root dry weight (Fig. 14) at the end of the experiment were greater for Chrysopogon aucheri than Cymbopogon jwarancusa in mixture when plants were equally defoliated zero, one, or two times. Cumulative shoot dry weight, crown dry weight, and root dry weight were similar for both species in monoculture under the same defoliation regimes, and in mixture and monoculture when plants were equally defoliated three times (Fig. 13 and 14).

Percent crude protein was comparable for both species in monoculture when the standing crop was clipped initially (1st clipping), and regrowth was clipped 4 weeks later (2nd clipping); however crude protein was greater for Chrysopogon aucheri than Cymbopogon jwarancusa when regrowth was clipped at subsequent 4-week intervals (3rd and final clippings) (Fig. 15 A). Digestibility of the standing crop at the initial clipping (1st clipping) and regrowth at the 3rd clipping was higher for Chrysopogon than Cymbopogon jwarancusa, and comparable for regrowth of both species at the 2nd and final clippings (Fig. 15 B).

In the 50:50 mixture when one species was defoliated zero, one, two or three times and the associated species was not defoliated, both species generally produced comparable numbers of tillers (Fig. 16 A, B, C, and D) and shoot dry weight (Fig. 17 A, B, and C) per plant. At week 40, Cymbopogon jwarancusa produced more tillers per plant

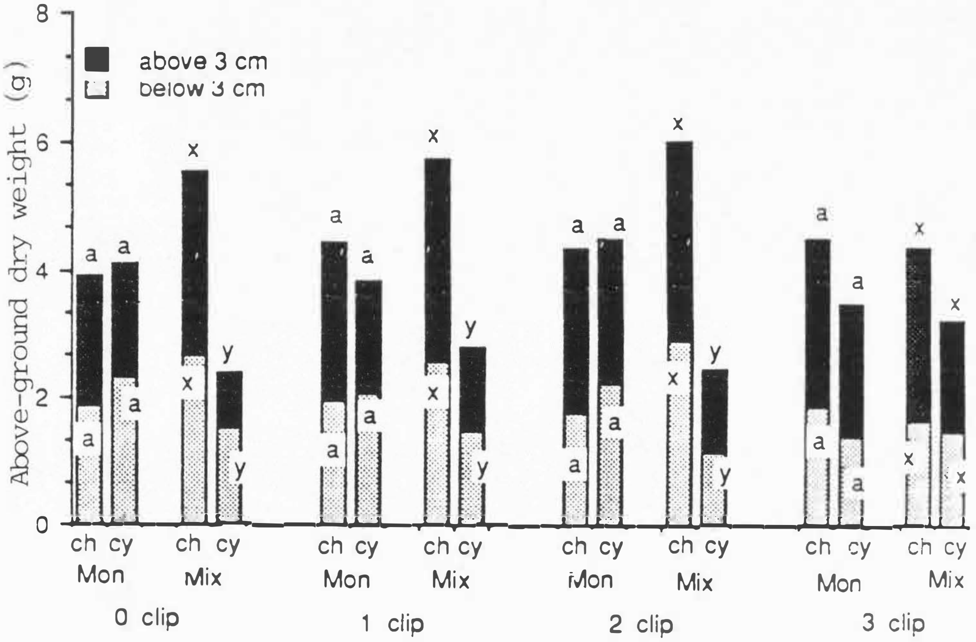


Figure 13. Above-ground dry weight (g) (cumulative shoot dry weight above 3-cm stubble height and crown dry weight below 3-cm) from 44-week-old Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in monoculture (Mon) and mixture (Mix) under different clipping regimes: 0 clip (control) = standing crop above 3-cm and crown below 3-cm clipped at 44 weeks (final harvest) after emergence; 1 clip = standing crop clipped at 32 weeks and regrowth and crown clipped at 44 weeks after emergence; 2 clip = standing crop clipped at 32 weeks, and regrowth clipped at 36 weeks, and regrowth and crown clipped at 44 weeks after emergence; 3 clip = standing crop clipped at 32 weeks, regrowth clipped at 36 and 40 weeks and regrowth and crown clipped at 44 weeks after emergence. Above 3-cm and below 3-cm dry weight values for species with different letters within monoculture or mixture under each clipping regime are significantly different ($LSD_{.05}$ = 1.7 for above 3-cm and .88 for below 3-cm; n = 4).

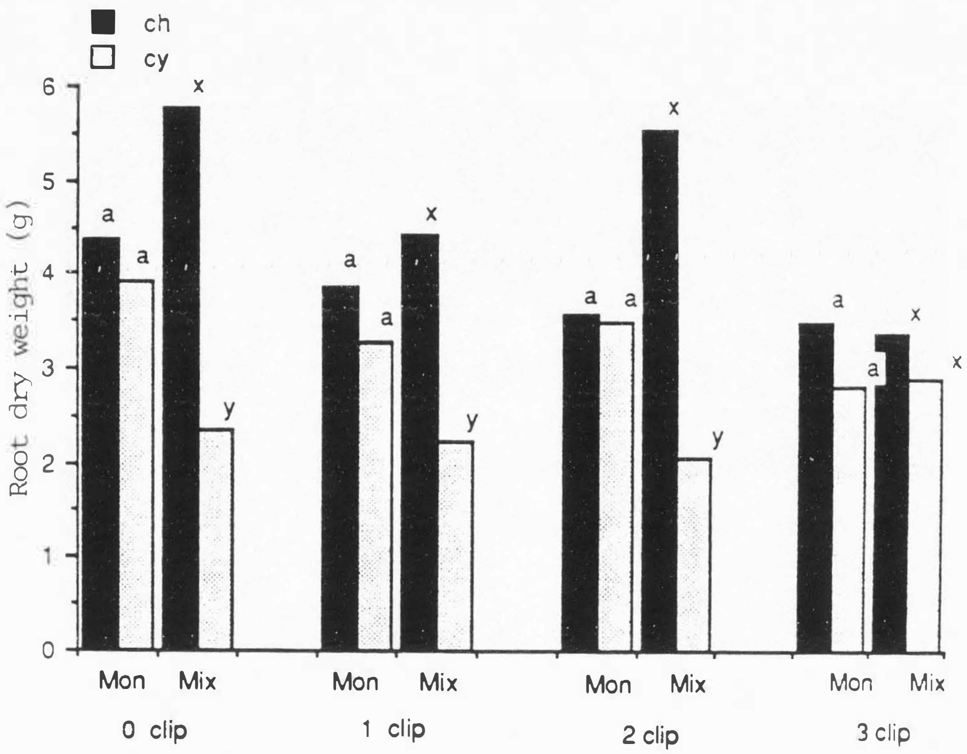


Figure 14. Mean root dry weight (g) harvested from 44-week-old Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in monoculture (Mon) and mixture (Mix) under different clipping regimes (3-cm stubble height): 0 clip (control) = standing crop clipped at 44 weeks (final harvest) after emergence; 1 clip = standing crop clipped at 32 weeks and regrowth clipped at 44 weeks after emergence; 2 clip = standing crop clipped at 32 weeks and regrowth clipped at 36 and 44 weeks after emergence; 3 clip = standing crop clipped at 32 weeks and regrowth clipped at 36, 40, and 44 weeks after emergence. Values for species with different letters within monoculture or mixture under each clipping regime are significantly different ($LSD_{.05}$ = 1.7; n = 4).

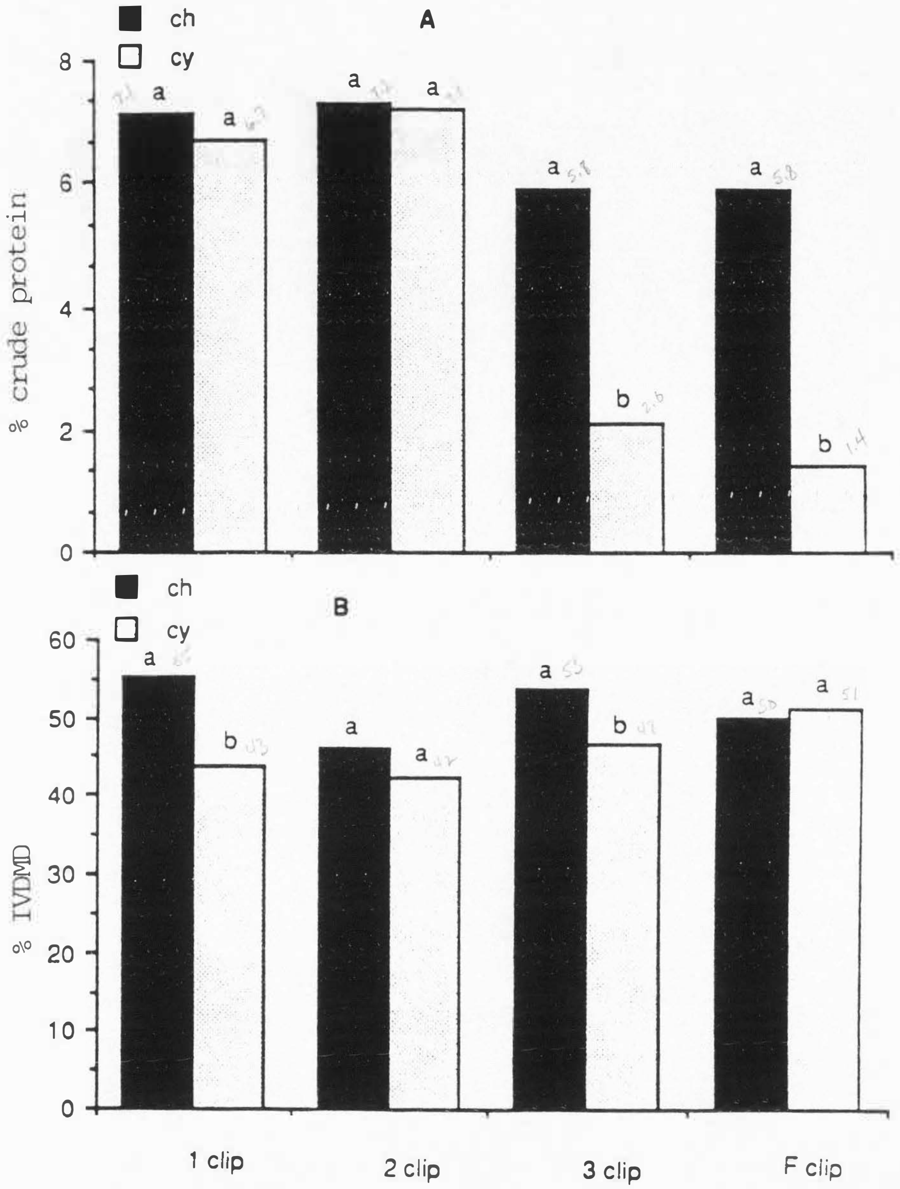
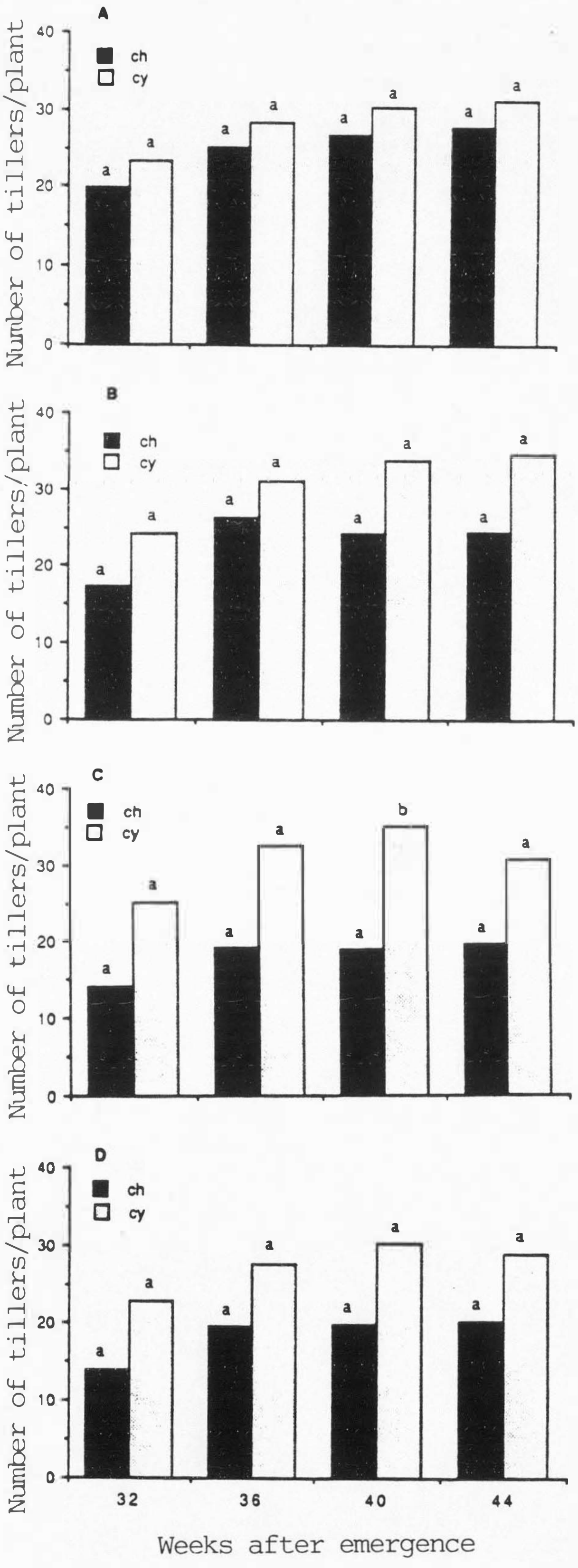


Figure 15. Mean percent crude protein (A) and percent in vitro digestible dry matter (% IVDMD) (B) for Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in monoculture under different clipping regimes (3-cm stubble height): 1 clip = initial standing crop clipped at 32 weeks after emergence; 2 clip = regrowth clipped at 36 weeks after emergence; 3 clip = regrowth clipped again at 40 weeks after emergence; and F clip = final regrowth clipped at 44 weeks after emergence. Values for species with different letters under each clipping regime are significantly different ($LSD_{.05}$ = 2.0 for A, 5.3 for B: n = 4).

Figure 16. Mean number of tillers per plant for *Chrysopogon aucheri* (Ch) and *Cymbopogon jwarancusa* (Cy) plants grown in mixture under different clipping regimes (each value represents a treatment where the species indicated is clipped to a 3-cm stubble height and the associated species is not clipped): (A) 0 clip (control); (B) 1 clip = standing crop of either species clipped at 32 weeks after emergence; (C) 2 clip = standing crop of either species clipped at 32 weeks and regrowth clipped at 36 weeks after emergence; and (D) 3 clip = standing crop of either species clipped at 32 weeks and regrowth clipped at 36 and 40 weeks after emergence. Values for species with different letters at each time interval are significantly different [$LSD_{.05}$ (A, B, C, and D) = 10.0 for 32 weeks, 12.0 for 36 weeks, and 12.8 for 40 and 44 weeks; n = 4].


A
B
C
D
ch
cy
Number of tillers/plant
0
10
20
30
40
a
b
32
36
40
44
Weeks after emergence

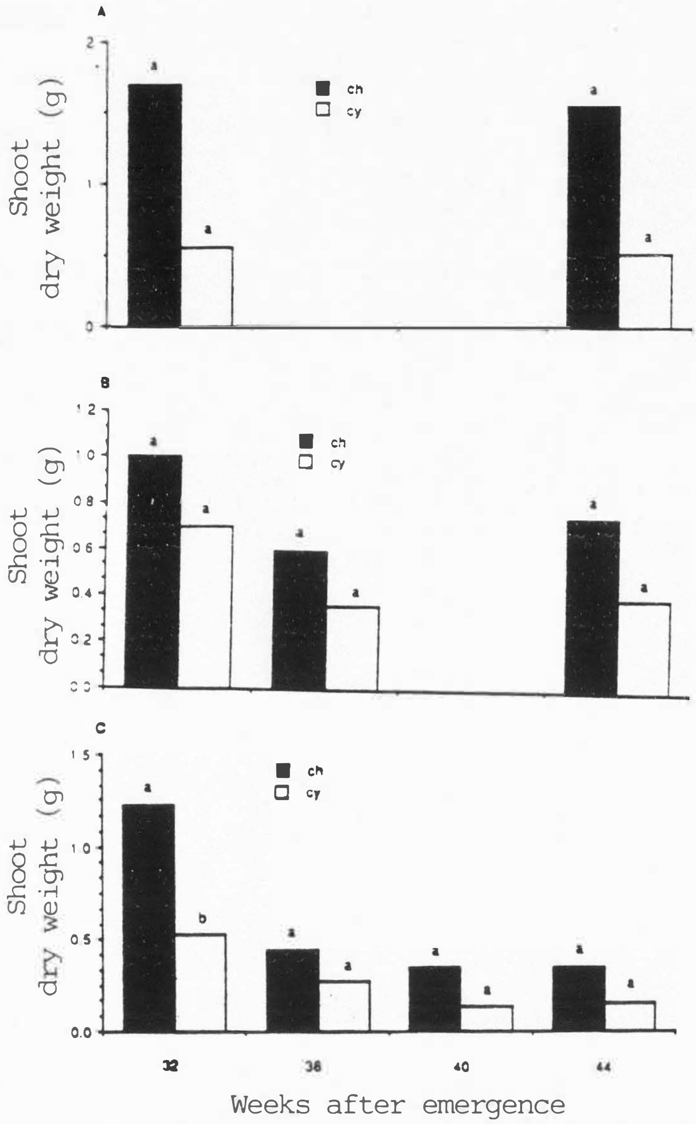


Figure 17. Mean shoot dry weight (g) of Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in mixture under different clipping regimes (each value represents a treatment where the species indicated is clipped to a 3-cm stubble height and the associated species is not clipped): (A) 1 clip = standing crop of either species clipped at 32 weeks and regrowth clipped at 44 weeks (final harvest) after emergence; (B) 2 clip = standing crop of either species clipped at 32 weeks and regrowth clipped at 36 and 44 weeks after emergence; and (C) 3 clip = standing crop of either species clipped at 32 weeks and regrowth clipped at 36, 40, and 44 weeks after emergence. Values for species with different letters at each time interval are significantly different [$LSD_{.05}$ (A, B, and C) = 0.61 for 32 weeks, 0.36 for 36 weeks, 0.22 for 40 weeks, and 0.53 for 44 weeks; n = 4].

than Chrysopogon aucheri when plants were defoliated two times (Fig. 16 C); and at week 32, Chrysopogon aucheri produced more shoot dry weight than Cymbopogon jwarancusa when plants were defoliated three times (Fig. 17 C). Cumulative shoot dry weight was greater for Chrysopogon aucheri than Cymbopogon jwarancusa when plants remained undefoliated or were clipped one time (Fig. 18), while crown dry weight and root dry weight were greater for Chrysopogon aucheri than Cymbopogon jwarancusa when plants were clipped zero, one two, or three times (Figs. 18 and 19).

Discussion

High tiller production, delayed elevation of apical meristems, and high vegetative:reproductive stem ratios are morphological characteristics associated with grazing tolerance (Branson 1953, Dahl and Hyder 1977, Richards and Caldwell 1985, Archer and Tieszen 1986, and Briske 1986). As in the 8-week seedling development experiment (Chapter III), Chrysopogon aucheri and Cymbopogon jwarancusa produced comparable numbers of leaves and tillers per plant during the early part of this experiment (up to 28 weeks after emergence). As plants matured (36 to 44 weeks after emergence), Cymbopogon jwarancusa produced more tillers per plant in monoculture than Chrysopogon aucheri under the different defoliation regimes. By the time defoliation treatments were implemented at 32 weeks after emergence,

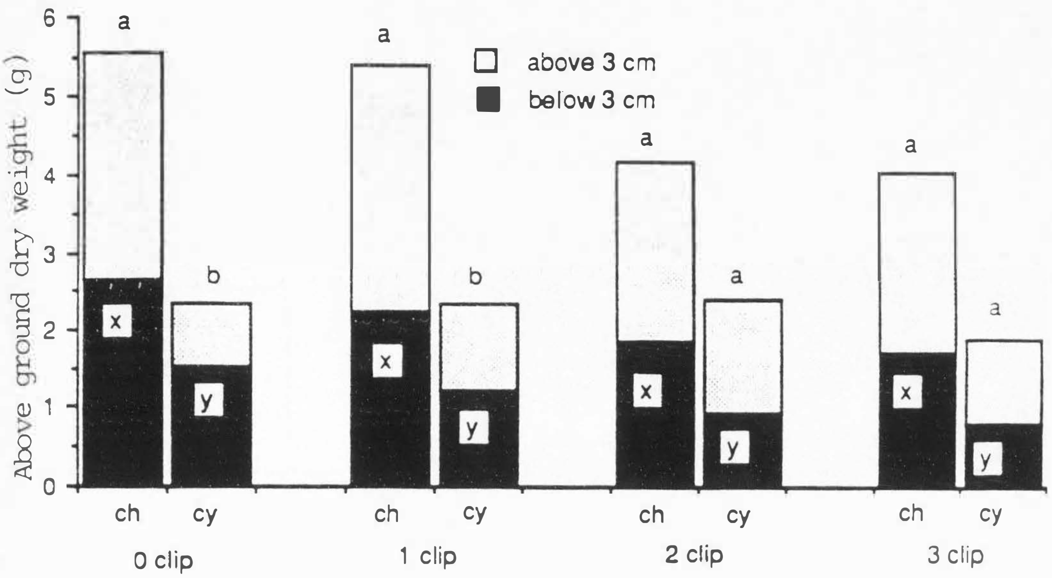


Figure 18. Above-ground dry weight (g) (cumulative shoot dry weight above 3-cm stubble height and below 3-cm) from 44-week-old Chrysopogon aucheri (Ch) and Cymbopogon jwarancusa (Cy) plants grown in mixture under different clipping regimes (each value represents a treatment where the species indicated is clipped to a 3-cm stubble height and the associated species is not clipped): 0 clip (control) = standing crop above 3-cm and crown below 3-cm clipped at 44 weeks (final harvest) after emergence; 1 clip = standing crop clipped at 32 weeks and regrowth and crown clipped at 44 weeks after emergence; 2 clip = standing crop clipped at 32 weeks, regrowth clipped at 36 weeks, and regrowth and crown clipped at 44 weeks after emergence; and 3 clip = standing crop clipped at 32 weeks, regrowth clipped at 36 and 40 weeks, and regrowth and crown clipped at 44 weeks after emergence. Values for species above 3-cm and below 3-cm with different letters under each clipping regime are significantly different ($LSD_{.05}$ = 1.7 for above 3-cm and .88 for below 3-cm; n = 4).

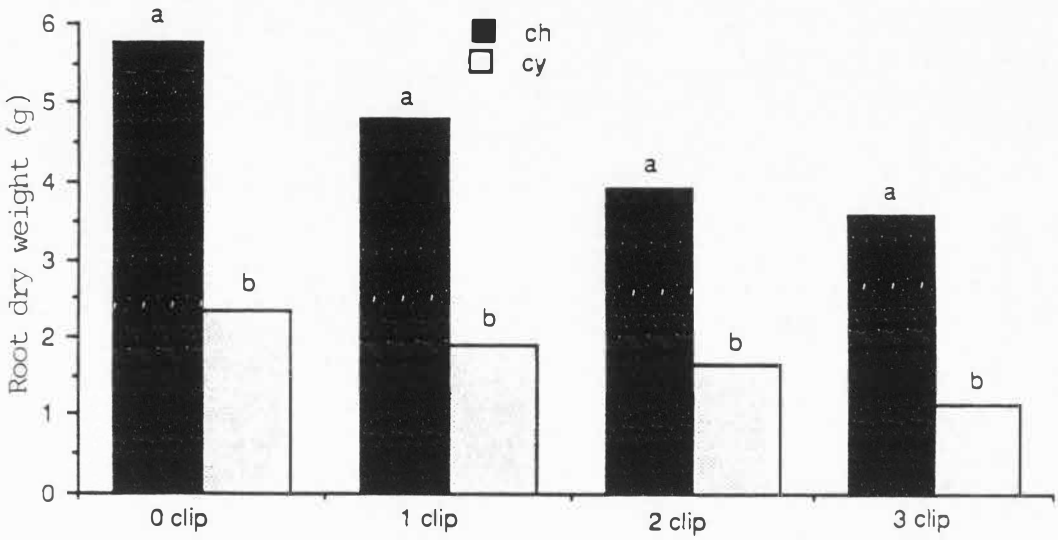


Figure 19. Mean root dry weight (g) harvested from 44-week-old Chrysopogon aucheri (Ch) and Cymbopogon Jwarancusa (Cy) plants grown in mixture under different clipping regimes (each value represents a treatment where the species indicated is clipped to a 3-cm stubble height and the associated species is not clipped): 0 clip (control) = standing crop clipped at 44 weeks (final harvest) after emergence; 1 clip = standing crop clipped at 32 weeks and regrowth clipped at 44 weeks after emergence; 2 clip = standing crop clipped at 32 weeks and regrowth clipped at 36 and 44 weeks after emergence; and 3 clip = standing crop clipped at 32 weeks and regrowth clipped at 36, 40, and 44 weeks after emergence. Values for species with different letters under each clipping regime are significantly different ($LSD_{.05}$ = 1.70; n = 4).

most of the main stems and a small proportion of secondary tillers on _Chrysopogon aucheri_ plants had elevated apical meristems and developed inflorescences. Leaf growth normally ceases on reproductive stems (Langer 1972, Dahl and Hyder 1977), and tillering from axillary buds can be slow following defoliation when water and nutrients are limiting (Branson 1953, Hyder 1972). However, water and nutrient augmentation in this controlled environment study may have allowed for greater tiller development following the defoliation of flowering _Chrysopogon aucheri_ plants than would be found under limiting field conditions. _Chrysopogon aucheri_ might have remained in a vegetative state longer if it had been defoliated before apical meristem elevation (Langer 1972). _Cymbopogon jwarancusa_ never elevated apical meristems, and continued to produce new tillers and extend partially defoliated leaves from intercalary meristems.

Several factors, including plant age, plant size, the accumulation of certain metabolites, temperature, light intensity, and photoperiod are involved in the transformation from the vegetative to the reproductive state in most grasses (Langer 1972). Mature plants of both species develop flowers and set seed during the same time period (March to May) under field conditions in Baluchistan (Cope 1982; Saleem, personal observation). However, no information is available on floral development of young plants of either species. In this greenhouse study in Logan (41 N latitude), Chrysopogon aucheri initiated flowering as early as 24 weeks after emergence in March when the day length is similar (approximately 12 h) to that in Quetta, Baluchistan (30 N latitude) in March (List 1948). Chrysopogon aucheri continued to develop inflorescences up to 32 weeks after emergence in May when the day length in Logan is up to 55 minutes longer than in Quetta (List 1948). Cymbopogon jwarancusa plants of similar age may not have flowered at the same time as the Chrysopogon aucheri in the greenhouse because they may require more time in a vegetative stage before floral induction can occur, or they may be more sensitive to variation in day length (Dahl and Hyder 1977). Certain species may detect day-length variations of less than 1 h that can delay or prohibit flowering (Dahl and Hyder 1977).

Plants having high reproductive to vegetative ratios can be easily removed from communities by excessive grazing (Branson, 1953, and Hyder 1972). Dahl and Hyder (1977) reported that several warm-season grasses were vulnerable to defoliation (i.e. removal of elevated apical meristem) when three-fourths to two-thirds of their stems were reproductive. In this study only 20 % of the stems of undefoliated Chrysopogon aucheri plants were reproductive. Therefore, Chrysopogon aucheri may not be that susceptible to grazing, even though some tillers elevate apical meristems.

The impact of defoliation on a plant varies, depending on the intensity, frequency, pattern, and timing of tissue removal (Branson 1953, Dahl and Hyder 1977, Archer and Tieszen 1986, Kalmbacher and Martin 1988). Kanodia et al. (1981) found that increasing the clipping height from 5 to 15 cm above the soil surface and increasing the clipping interval from 10 to 60 days increased aboveground biomass production of Chrysopogon fulvus in India. In the present study, clipping at a 3-cm stubble height at 4-week intervals did not decrease tiller development and did not result in significant decreases in aboveground biomass production for both species. This is not the case on unmanaged rangelands in Baluchistan where frequent, intensive grazing at any time during the growing season can decrease or eliminate Chrysopogon aucheri in grassland communities. Even though controlled environment conditions do not fully represent field conditions in Baluchistan, plant responses to the different defoliation treatments indicate that Chrysopogon aucheri could be maintained in communities when frequency and intensity of grazing are regulated.

Clipping does not completely mimic herbivore because of the manner in which plant parts are selected and removed from the plant. The pattern of defoliation greatly affects the canopy structure and microenvironment of the plant, which influence defoliation responses (McNaughton 1986, Caldwell et al. 1983, Gold and Caldwell 1990, Wallace 1990). In the present study, however, the uniform pattern of defoliation may simulate grazing more closely than in other clipping studies because the scarcity of vegetation on Baluchistan rangelands may not allow grazing animals to be very selective (FAO 1981).

Plant response to defoliation also varies with the level of competition from surrounding plants. Pemadasa and Amarasinghe (1982), working in a Cymbopogon - Themeda grassland in Sri Lanka, found that clipping reduced the competitive ability of Themeda trimula and resulted in greater biomass production in associated Cymbopogon species. In the present study, when both species were defoliated equally and less frequently (zero, one, or two clippings) Chrysopogon aucheri produced more shoot and root biomass than Cymbopogon jwarancusa in mixture. However, under a higher frequency of defoliation (3 clippings) the competitive advantage of Chrysopogon aucheri was not evident in mixture, as both species produced comparable amounts of shoot and root biomass. When one species was defoliated zero to three times in mixture and the associated species was not defoliated, Chrysopogon aucheri was comparable to Cymbopogon jwarancusa in tiller development and shoot and root biomass production, and superior in root biomass production. Even though growing conditions were more favorable in the greenhouse than in the field in Baluchistan, results indicate that Chrysopogon aucheri could coexist with Cymbopogon jwarancusa in the field if the intensity and frequency of defoliation by livestock was managed more effectively.

Chrysopogon aucheri may be similar to species such as Schizachyrium scoparium, Bouteloua curtipendula, and Koeleria cristata, which are tolerant of moderate grazing, but still decrease in grazed communities because of their relatively high palatabilities (Dahl and Hyder 1977). Palatability generally decreases with age in many grasses, particularly when plants go reproductive (Hodgson 1982). Despite going reproductive, Chrysopogon aucheri was comparable or higher (depending upon sampling date) in crude protein content and digestibility than Cymbopogon jwarancusa when frequently defoliated. However, the presence of essential oils in the foliage of Cymbopogon jwarancusa overrides nutritional differences when comparing the relative palatability of the two species.

Although not measured in this study, the essential oil content of Cymbopogon jwarancusa is regarded as an avoidance mechanism (Briske 1986) that greatly reduces the frequency and intensity of grazing of this species under unmanaged conditions (West Pakistan Forest Department 1960). Chopra et al. (1956) demonstrated that apart from being an essential oil-bearing plant, Cymbopogon jwarancusa was a nutritious grass. Similarly, Ghosh and Mathur (1962) indicated that after the extraction of essential oils, Cymbopogon flexuous had a higher palatability than wheat or rice straw. More research is required under grazing conditions in the field to more accurately determine the effects of grazing tolerance and grazing avoidance on Chrysopogon aucheri - Cymbopogon jwarancusa interactions and to develop guidelines for more 'prudent' grazing.

CHAPTER V

SYNTHESIS

Under field conditions in Baluchistan, continuous season-long or year-long grazing by livestock (sheep, goats, camels, and cattle) has led to the gradual replacement of *Chrysopogon aucheri* by *Cymbopogon jwarancusa.* Species interactions have been primarily related to different grazing responses, i. e. the more palatable *Chrysopogon aucheri* being defoliated more intensively and frequently than the less palatable *Cymbopogon jwarancusa.* Three experiments were conducted in controlled environments to determine how germination, seedling development, and defoliation tolerance influence the growth and development of these two species.

Cymbopogon jwarancusa was superior to *Chrysopogon aucheri* in the germination phase in experiment 1. *Cymbopogon jwarancusa* had more filled seeds with higher viability than *Chrysopogon aucheri.* *Cymbopogon jwarancusa* had significantly higher cumulative germination in five of six alternating temperature regimes and a faster rate of germination in colder temperature regimes when both species started germination. The temperature regimes represent field temperatures during the normal recruitment period in Baluchistan. Germination at colder temperature regimes may allow *Cymbopogon jwarancusa* to have better recruitment than Chrysopogon aucheri under field conditions when soil moisture is more readily available.

In general, seedlings of both species were comparable in terms of shoot and root development over a 60-day growing period in experiment 2. When differences occurred, Chrysopogon aucheri seedlings were more vigorous than seedlings of Cymbopogon jwarancusa. Chrysopogon aucheri developed a greater number, length, and dry weight of primary and seminal roots than Cymbopogon jwarancusa at 30 and 60 days after emergence, respectively. Chrysopogon aucheri also had greater adventitious root length at 60 days after emergence than Cymbopogon jwarancusa. Superiority in root elongation may allow Chrysopogon aucheri seedlings the advantage of better survival in the field than Cymbopogon jwarancusa seedlings provided that Chrysopogon aucheri is not grazed at the seedling stage.

Rapid adventitious root development on seedlings of both species in a controlled environment indicates high potential for successful establishment. However, elongation of the subcoleoptile internode and root development on the subcoleoptile internode indicates that both species have "panicoid" type seedlings. Panicoid seedlings can have establishment problems in arid regions where low moisture near the soil surface may limit adventitious root development.

Both species had comparable leaf and tiller development as long as they remained in a vegetative state without defoliation. However, under the conditions of experiment 3 most of the main stems of Chrysopogon aucheri elevated apical meristems as early as 24 weeks after emergence and flowered before the first defoliation event 32 weeks after emergence.

Defoliation responses of the two species varied in experiment 3, depending upon the frequency of defoliation and whether a species was grown in mixture or monoculture. Cymbopogon jwarancusa produced more tillers per plant than Chrysopogon aucheri when both species were equally defoliated one, two, or three times in monoculture, where as Chrysopogon aucheri produced greater shoot and root biomass than Cymbopogon jwarancusa when both species were equally defoliated one, or two times in mixture. When one species was defoliated one, two, or three times and the associated species was not defoliated, shoot biomass was comparable for both species but Chrysopogon aucheri had greater root biomass than Cymbopogon jwarancusa. Thus, it is difficult to claim that one species has a distinct advantage over the other under the conditions of this study.

Results from these controlled environment experiments cannot be directly interpolated to the field conditions in Baluchistan, but they do provide some insights about the growth and development and interaction of *Chrysopogon aucheri* and *Cymbopogon jwarancusa.* If a *Chrysopogon-Cymbopogon* grassland was protected from grazing, it appears that *Cymbopogon jwarancusa* would have greater recruitment potential than *Chrysopogon aucheri.* However, once seeds of both species germinated, it appears that seedlings and more mature plants of *Chrysopogon aucheri* would be comparable in growth and development to those of *Cymbopogon jwarancusa.* Despite its higher palatability, *Chrysopogon aucheri* should be able to co-exist with *Cymbopogon jwarancusa* if frequency and intensity of defoliation are carefully controlled. More research needs to be conducted to more fully understand the relationship between *Chrysopogon aucheri* and *Cymbopogon jwarancusa* under field conditions. Specific research needs include: floral development and seed set, seedling recruitment, adventitious root development on seedlings under water-limited conditions, quantification of oil content of *Cymbopogon jwarancusa* at different growth stages, and monitoring the intensity and frequency of defoliation of grasses under different livestock grazing systems.

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APPENDIX

Table 5. Mean monthly maximum and minimum temperature and monthly precipitation data for Quetta, Baluchistan.

Month	Max. temp.(^{o}C)	Min. temp. (^{o}C)	Rainfall mm
Jan	10.8	- 2.8	38.8
Feb	13.4	- 1.2	63.7
Mar	18.4	3.1	42.4
Apr	24.7	7.3	12.4
May	30.4	10.8	6.3
Jun	34.2	14.2	1.3
Jul	35.4	18.9	18.3
Aug	34.3	16.4	4.3
Sep	31.2	9.8	0.5
Oct	25.0	3.2	1.3
Nov	18.0	- 1.8	5.6
Dec	13.0	- 3.7	22.9

Table 6. Heavy defoliation (85% removal) regimes for monocultures and 50:50 mixtures of _Chrysopogon aucheri_ (Ch) and _Cymbopogon jwaracusa_ (Cy).

Sequence of defoliation	_Chrysopogon_[1] (monoculture)	_Chrysopogon Cymbopogon_[1] (50:50)	_Cymbopogon_[1] (monoculture)
No defoliation (0)[2]	Ch (0)	Ch (0) & Cy (0)	Cy (0)
Initial (1)		Ch (1) & Cy (0)	
		Ch (0) & Cy (1)	
	Ch (1)	Ch (1) & Cy (1)	Cy (1)
Initial (1) + regrowth (2)		Ch (2) & Cy (0)	
		Ch (0) & Cy (2)	
		Ch (2) & Cy (2)	
		Ch (2) & Cy (1)	
	Ch (2)	Ch (1) & Cy (2)	Cy (2)
Initial (1) + regrowth (2) + regrowth (3)		Ch (3) & Cy (0)	
		Ch (0) & Cy (3)	
		Ch (3) & Cy (3)	
		Ch (3) & Cy (1)	
		Ch (1) & Cy (3)	
		Ch (3) & Cy (2)	
	Ch (3)	Ch (2) & Cy (3)	Cy (3)

[1]Four plants per pot; four replications (pots) per treatment.

[2]Numbers in parentheses represent defoliation frequencies of the initial standing crop and regrowth; i.e. 0 clip (control) = standing crop clipped at 44 weeks (final harvest) after emergence; 1 clip = standing crop clipped at 32 weeks and regrowth clipped at 44 weeks after emergence; 2 clip = standing crop clipped at 32 weeks and regrowth clipped at 36 and 44 weeks after emergence; and 3 clip = standing crop clipped at 32 weeks and regrowth clipped at 36, 40, and 44 weeks after emergence.

VITA

Mohammad Saleem

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Autecological characteristics of *Chrysopogon aucheri* and *Cymbopogon jwarancusa*, dominant rangeland grasses in Balucistan.

Major Field: Range Science

Biographical Information:

Personal Data: Born at Village Ahmadidargah, District Zhob, Baluchistan (Pakistan), February 2, 1950, Son of Salim Khan and Syeeda-Lo.

Education: Received Intermediate and Secondary Education from Govt. Intermediate College Fortsandeman in 1969; received a Bachelor of Science in Forestry from University of Peshawar, September, 1974; received a Master of Science in Forestry from University of Peshawar September, 1981; completed requirements for a Doctor of Philosophy in Range Science at Utah State University, June 1990.

Professional Experience: 1990---Divisional Forest Officer, Forest Department Baluchistan (Pakistan); 1986 - 1990 Graduate Fellow, Department of Range Science, Utah State University, Logan, Utah; 1974 - 1986 Range Forest Officer and Divisional Forest Officer, Forest Department, Baluchistan (Pakistan).