ECOLOGY OF *CHRYSOPOGON AUCHERI* AND *CYMBOPOGON JWARANCUSA*. III. MORPHOLOGY AND DEFOLIATION RESPONSE

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SUMMARY

Little is known about the defoliation responses of the palatable grass *Chrysopogon aucheri* (Boiss.) Stapf., and the co-occurring unpalatable grass, *Chymbopogon jwarancusa* (Jones) Schult., 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 associated species. The final harvest of all plants in every defoliation treatment occurred at 44 weeks after emergence. Response to defoliation was measured in terms off leaf and tiller development and shoot and root biomass production. 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*

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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, one, two, or three 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 (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, 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 sward 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 plants (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* (Jones) Schult. is not readily grazed because of a high essential oil content, comprised primarily of piperidine (Chopra et al. 1956, Saeed et al. 1978).

In Balochistan, *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 behaviour 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* (Boiss.) Stapf. are often more frequently and intensively defoliated than less palatable species such as *Cymbopogon jwarancusa*. 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.

MATERIAL AND METHODS

This experiment was conducted in a greenhouse under natural light conditions in Logan, Utah, USA, 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 posts (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 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. 1). 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). 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.

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 posts, 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 % 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. 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

Both species had similar patterns of leaf and tiller development in monoculture or mixture until 24 weeks after emergence. At that time, plants had 13 to 17 tillers per plant with 4 to 5 leaves per tiller. *Chrysopogon aucheri* plants elongated apical meristems on main stems as early as 24 weeks after emergence. By week 32 when defoliation treatments were implemented, 75% of

Figure - 1

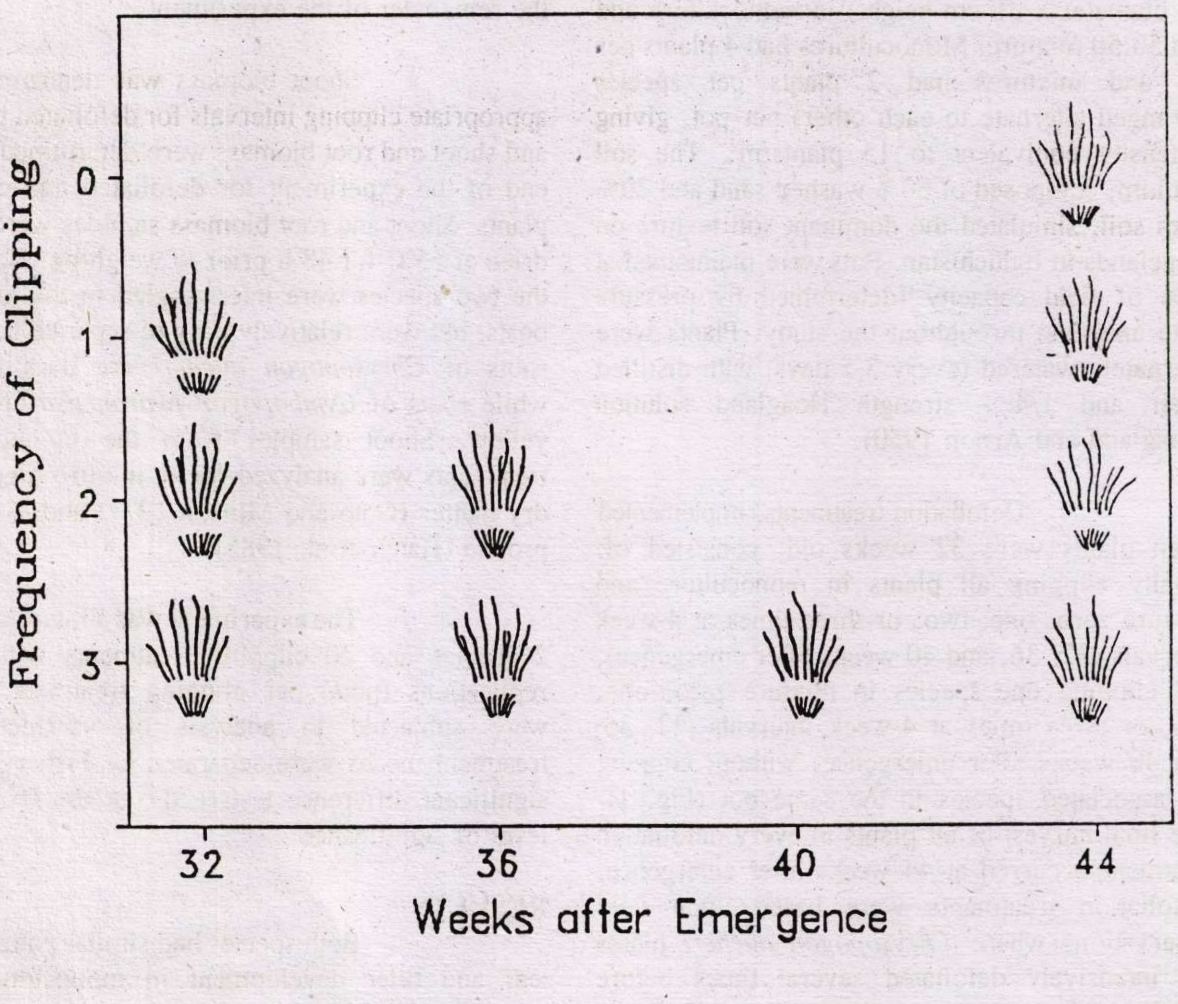
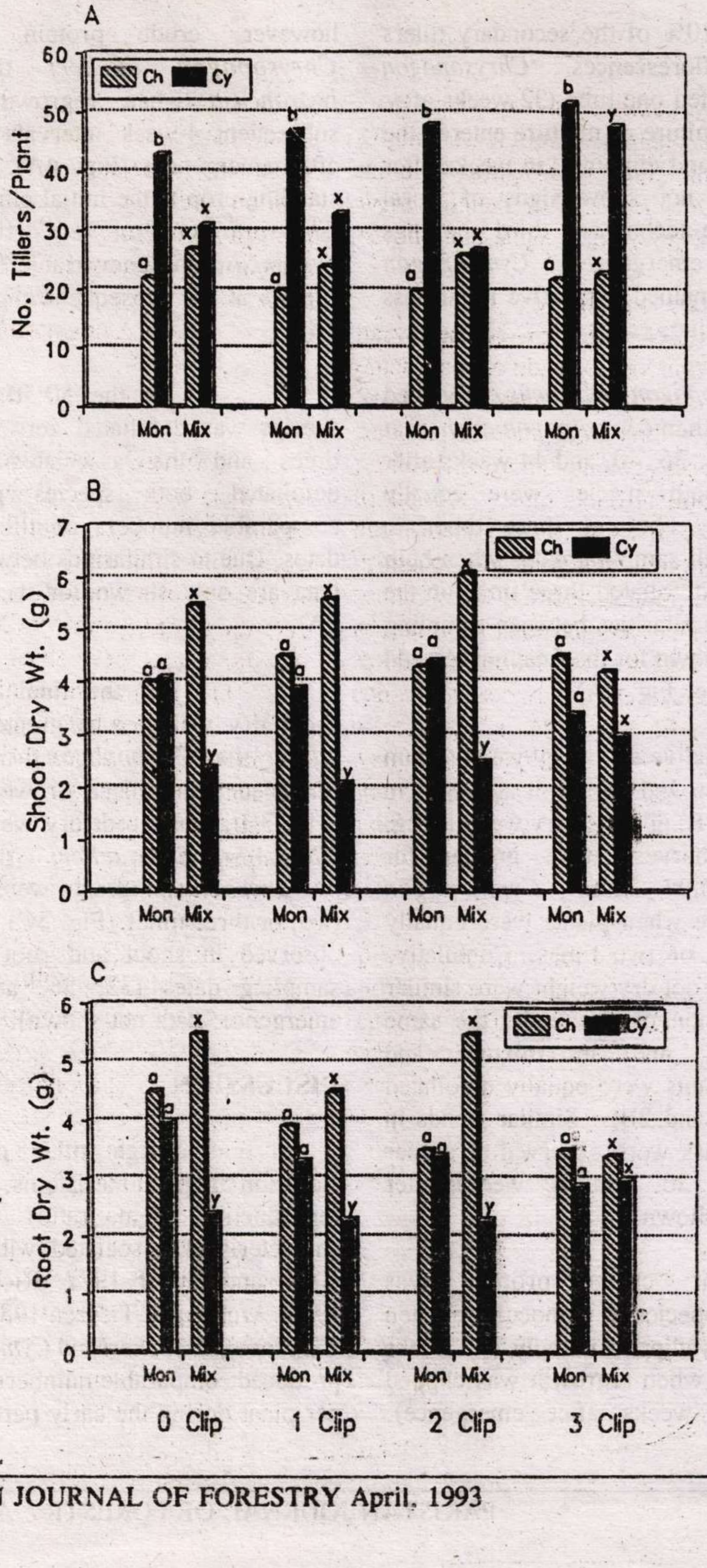

Frequency of Clipping
0
1
2
3
32
36
40
44
Weeks after Emergence

Figure - 2



A
No. Tillers/Plant
Ch
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Mon
Mix
B
Shoot Dry Wt. (g)
C
Root Dry Wt. (g)
0 Clip
1 Clip
2 Clip
3 Clip

the main stems and 10% of the secondary tillers 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.

Cymbopogon jwarancusa produced more tillers per plant than *Chrysopogon aucheri* at all sampling dates (32, 36, 40, and 44 weeks after emergence) when both species were equally defoliated zero, one, two, or three times in monoculture, and at all sampling dates when both species were equally defoliated three times in the mixture. Due to the similarities between sampling dates, data are only shown for the final harvest (44 weeks after emergence, Fig. 2A).

Cumulative shoot dry weight (sum of initial standing crop and regrowth above 3-cm stubble height) (Fig. 2B) and root dry weight (Fig. 2C) at the final harvest were greater for *Chrysopogon aucheri* than *Cymbopogon jwarancusa* in mixture when plants were equally defoliated zero, one, or two times. Cumulative shoot 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. 2A and 2B). Similar trends in root and shoot biomass were observed at earlier sampling dates (32, 36, and 40 weeks after emergence; data not shown).

Percent crude protein was comparable for both species in monoculture when the standing crop was clipped initially (32 weeks after emergence) and when regrowth was clipped 4 weeks later (36 weeks after emergence); however, crude protein was greater for *Chrysopogon aucheri* than *Cymbopogon jwarancusa* when regrowth was clipped at subsequent 4-week intervals (40 and 44 weeks after emergence) (Fig. 4A). Digestibility of the standing crop at the initial clipping was higher for *Chrysopogon aucheri* than *Cymbopogon jwarancusa* and comparable for regrowth of both species at the subsequent clipping intervals (Fig. 4B).

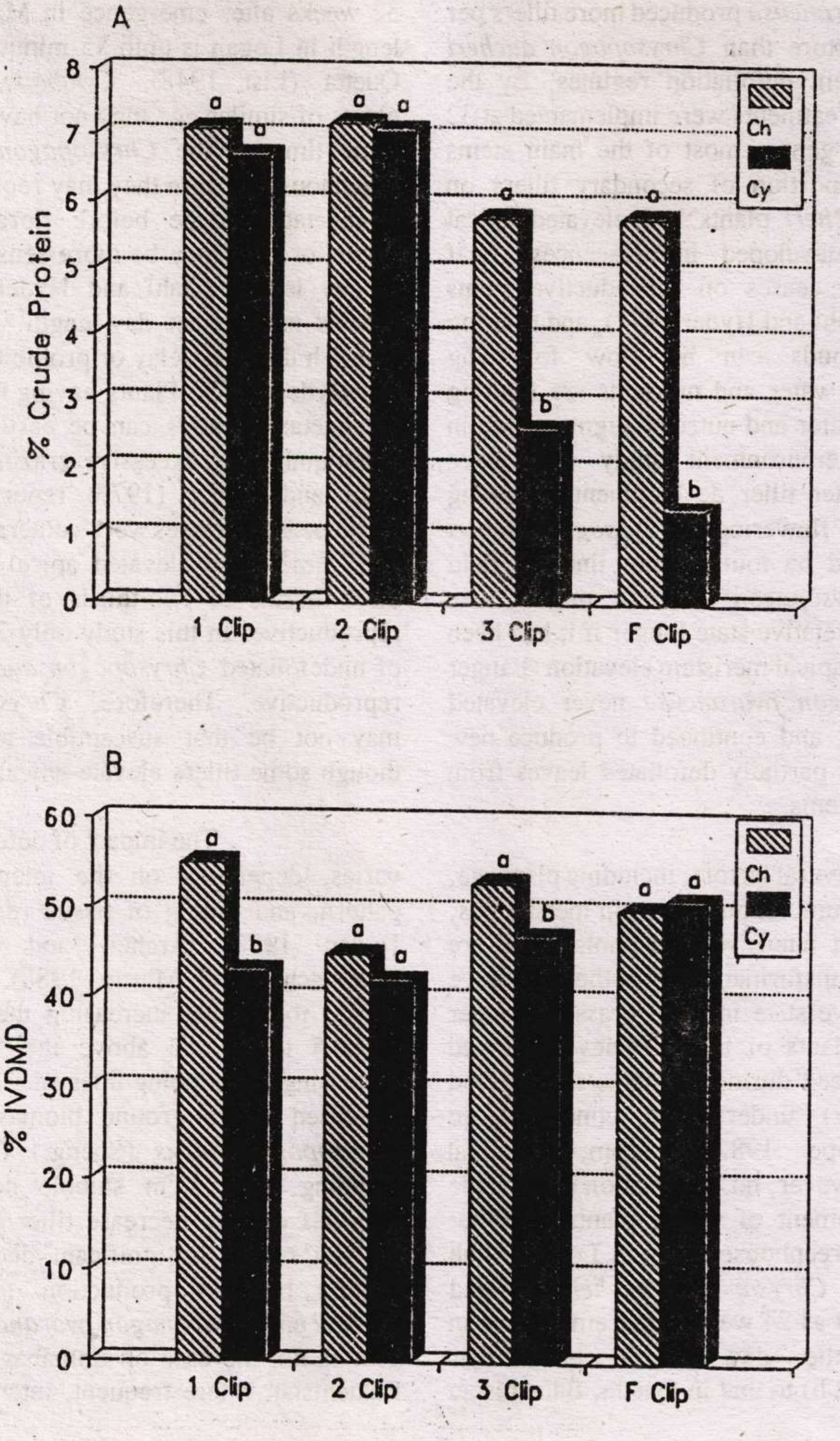
In the 50:50 mixture when one species was defoliated zero, one, two or three times and the associated species was not defoliated, both species generally produced comparable numbers of tillers at all sampling dates. Due to similarities between sampling dates, data are only shown for the final harvest (Fig. 3A).

At the final harvest, cumulative shoot dry weight was greater for *Chrysopogon aucheri* than *Cymbopogon jwarancusa* when plants remained undefoliated or were clipped one time (Fig. 3B), while root dry weight was greater for *Chrysopogon aucheri* than *Cymbopogon jwarancusa* when plants were clipped zero, one, two, or three times (Fig. 3C). Similar trends were observed in shoot and root biomass at earlier sampling dates (32, 36, and 40 weeks after emergence; data not shown).

DISCUSSION

High tiller production, delayed elevation of apical meristems, and high vegetative: reproductive stem ratios are morphological characteristics associated with grazing tolerance (Dahl and Hyder 1977, Richards and Caldwell 1985, Archer and Tieszen 1986, and Briske 1986). *Chrysopogon aucheri* and *Cymbopogon jwarancusa* produced comparable numbers of leaves and tillers per plant during the early part of this experiment

Figure - 3



A
% Crude Protein
0
1
2
3
4
5
6
7
8
a
a
a
a
a
b
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b
Ch
Cy
1 Clip
2 Clip
3 Clip
F Clip
B
% IVDMD
0
10
20
30
40
50
60
a
b
a
a
a
b
a
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Ch
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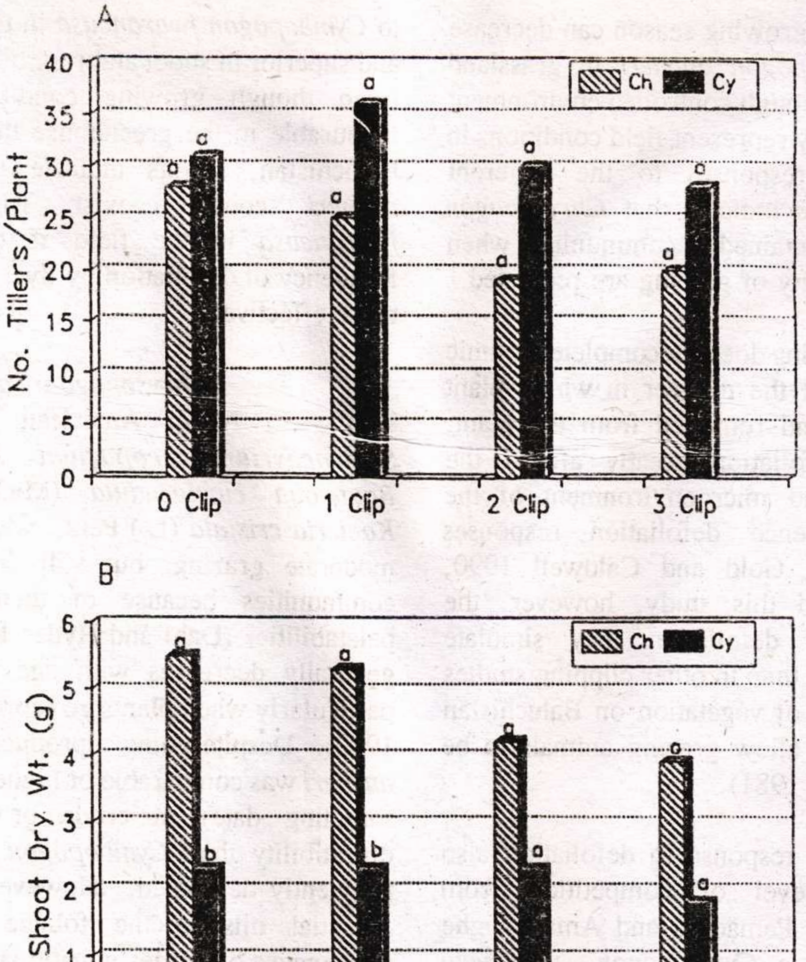
1 Clip
2 Clip
3 Clip
F Clip

(upto 24 weeks after emergence); however, 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, 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 (Hyder 1972). 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 developed 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, Utah (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 upto 32 weeks after emergence in May when the day length in Logan is upto 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 (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 (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 above ground biomass production of *Chrysopogon fulvus* (Speng.) Chiov. in India. Clipping at a 3-cm stubble height at 4-week intervals did not decrease tiller development and did not result in significant decreases in above ground biomass production for *Chrysopogon aucheri* and *Cymbopogon jwarancusa* in this study. This is not the case on unmanaged rangelands in Baluchistan where frequent, intensive grazing at

Figure - 4


A
Ch
Cy
No. Tillers/Plant
40
35
30
25
20
15
10
5
0
a
0 Clip
1 Clip
2 Clip
3 Clip
B
Shoot Dry Wt. (g)
6
5
4
3
2
1
0
b
C
Root Dry Wt. (g)
7

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, Gold and Caldwell 1990, Wallace 1990). In this 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* Forsk. 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 superior in shoot and root biomass production. Even though growing conditions were more favourable in the greenhouse than in the field in Balochistan, 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 North American grasses such as *Schizachyrium scoparium* (Michx.) Nash, *Bouteloua curtipendula* (Michx.) Torr., and *Koeleria cristata* (L.) Pers., 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 flexuosus* (Nees) Stapf. 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.

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FIGURE CAPTIONS

Figure 1. Defoliation treatments for *Chrysopoqon 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 cliop= standing crop clipped 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.

Figure 2. Mean number f tillers per plant (A), shoot dry weight (B), and root dry weight (c) for *Chrysopogon aucheri* (Ch) and *Cymbopogon jwarancusa* (y) plants after 44 weeks in monoculture (Mon) and mixture (Mix) under different clipping regimes: 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 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 are significantly different ($LSD_{.05}$).

Figure 3. 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: 1 clip = standing crop clipped at 32 weeks after emergence; 2 clip = regrowth clipped at 36 weeks after emergence; 3 clip = regrowth clipped at 40 weeks after emergence. F clip = final regrowth clipped at 44 weeks after emergence. Values for species with different letters under each clipping regime are significantly different ($LSD_{.05}$).

Figure 4. Mean number of tillers per plant (A), shoot dry wight (B), and root dry weight (C) for *Chrysopogon aucheri* (Ch) and *Cymbopogon jwarancusa* (Cy) after 44 weeks in mixture under different clipping regimes (each value represents a treatment where the species indicated is clipped and the associated species is not clipped): 0 clip (control) = standing crop clipped at 44 weeks (final harvest) after emergence; 1 clip = standing crop of either species clipped at 32 weeks and regrowth clipped at 44 weeks after emergence; 2 clip = standing crop of either species clipped at 32 weeks and regrowth clopped at 36 and 44 weeks after emergence; and 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 under each clipping regime are significantly different ($LSD_{.05}$)).

NEWS AND VIEWS

Plantations and Climate Change

One of the most intensively studied large scale problems is the change in global climate. A global rise in temperature of about 0.3-4°C/10 years may be expected after the year 2000,