

EFFECTS OF NINE YEARS OF MOWING ON
TALLGRASS PRAIRIE GRASSLAND
COMMUNITY
&
REVIEW OF THE ECOLOGY OF
MONTANE GRASSLANDS
OF THE WESTERN
GHATS

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PREFACE

Grasslands are among the worlds most common yet least appreciated vegetation types. Grasslands have often been heavily exploited worldwide for agricultural and ranching, with most grasslands around the world fast losing place to various human activities the opportunity to fully understand these dynamic vegetation type is being lost. Studies on grasslands worldwide have shown that unlike previously thought grasslands are highly dynamic, species rich systems with a complex ecology. Studying grasslands can hence be a highly instructive endeavor and also provide new insights into natural systems. More significantly, studying and understanding grassland ecology is highly require if one wants to save the remaining natural and semi-natural grasslands.

The thesis work reported here as part of master's degree requirement is primarily directed towards understanding grassland systems; their ecology, dynamics and conservation. In the first chapter the focus is on understanding how mowing modulates species richness and composition of a grassland community. The long term mowing experiment study with data collected during a nine year period was used to understand dynamics of a grassland community through time under a mowing regime of varying frequencies of mows per year. The study sheds light on how frequency and seasonality of disturbances influence grassland community, and further it informs of the potential of long term effects of mowing. The second chapter is a review work on the montane grasslands of Western Ghats, in south India. The Western Ghats is a well recognized

biodiversity hotspot region along with the Sri Lankan archipelago. The main focus in my review is to find how much is known about the ecology of the montane grassland community and how far the present understanding is applicable to the conservation of these grasslands. While, at first glance the two chapters may appear almost unconnected, I might stress that the main motivation behind the second chapter was derived while working on the first chapter. In other words, the second chapter is an extension of the ecological ideas explored in the first chapter applied to a similar vegetation system at a different geographical location. I believe that given the amount of ecological understanding gained from studies on North American grasslands, the broad generalizations and facts about grasslands communities in general could provide a powerful cue for understanding poorly studied grassland systems elsewhere.

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**Effects of mowing on species richness and composition of an Oklahoma
grassland community over a nine year period**

Introduction

The role of disturbance in determining plant community structure and composition by altering availability of limiting resources and removing biomass is well recognized (Connell 1978; Pickett & White 1985). This is exemplified in grassland systems, where disturbances such as grazing and fire are crucial for maintaining species diversity (Collins 1987; Collins et al. 1998; Knapp et al. 1999). Long term studies on tallgrass prairie document the role played by fire and grazing in maintaining a dynamic and highly diverse ecosystem (Knapp et al. 1998). Although anthropogenic, mowing is similar to most natural disturbances in that it removes biomass and alters resource availability. Moreover, mowing is considered to mimic grazing with respect to effects on grassland species richness and composition (Collins et al. 1998). Several studies have demonstrated that mowing is both a tool for managing grasslands (Gibson et al. 1995; Collins et al. 1998; Clark & Wilson 2001; Stammel et al. 2003) and an experimental tool for investigating the role disturbances play in grassland dynamics (Armesto & Pickett 1985; Güsewell et al. 1998; Lepš 1999). While there are several studies on the effects of different frequencies and season of mowing on grassland communities worldwide (Hover & Bragg 1981; Collins et al. 2001; Güsewell & Le Nédic 2004; Antonsen & Olsson 2005), long-term studies have been relatively fewer in number (Güsewell et al. 1998, Fynn et al. 2004). Most of these studies have reported that mowing frequency and season of mowing affect species composition strongly, while species richness is less affected (Hover & Bragg 1981; Zobel et al. 1996; Güsewell & Le Nédic 2004).

The Intermediate Disturbance Hypothesis (IDH) theoretically encapsulates the role of disturbance in modulating species richness (Connell 1978; Huston 1979) and for

years it has been the guiding force for most studies involving disturbances. Frequency (number of disturbances per unit time) is one among several characterizations of disturbance regime (Shea et al. 2004). In principle, too frequent disturbances create conditions of high stress allowing only few species to survive, while too infrequent disturbances will allow dominance by a few species and competitive exclusion of the rest (Grime 1973; Huston 1979). Disturbance almost always enhances species richness except in conditions of low productivity (Proulx & Mazumder 1998), and this is also true in the case of mowing (Zobel et al. 1995; Lepš 1999; Kotowski & van Diggelen 2004). However the effect of different disturbance frequency on species richness is not always as predicted by IDH; it depends heavily on how the frequency of disturbance relates to plant lifespan (Shea et al. 2004). Compared to species richness, changes in species composition are mostly affected by the difference in growth habits and life-histories of plants in the community (Clark & Wilson 2001; Stammel et al. 2003).

Besides frequency, the timing of disturbance affects grasslands with pronounced seasonality. Studies have documented that the timing (or season) of disturbance affects composition by giving a competitive edge to those species which either grow or seed outside the disturbance period (Howe 1994) and this could possibly be true for mowing too. Management practices like mowing and prescribed burning often takes this into account by implementing them during the non-growing dormant season (Howe 1994; Collins 2000; Güsewell & Le Nédic 2004).

As previously mentioned, long-term studies on mowing are relatively few in number. The Konza LTER site is one of the best examples of long-term research on tallgrass prairie grasslands, however most of the research concerns fire and grazing

regimes. Compared to short term studies, long-term experiments detect slow and infrequent changes which become apparent only after a certain stretch of time (Franklin 1987). As far as disturbance and ecosystem response to disturbance is concerned long-term data provide a baseline by which predictions and decisions can be made (Turner et al. 2003). There is no minimum time-scale for calling a study long-term, but Güsewell et al. (1998) suggest that rate of fluctuations in ‘background’ dynamics and degree of association between the disturbance and the response variable be considered while deciding the length of an experimental study. According to Tilman (1989) most experimental studies are of 3 years or lesser duration, thus any study longer than 3 years in time scale could be considered long-term.

In this study, we use data collected from a nine year mowing experiment to show the effects of mowing seasonality and frequency on species richness and composition. The nine year period of the mowing experiment provides an opportunity to look for the possibility of long-term effects. More specifically, we shall address the following questions; (a) Does mowing frequency and season of mowing alter species richness? (b) How does mowing frequency, season of mow and time-period of mowing affect species composition? (c) Is there any discernible long-term effect of mowing on the species composition? We were also interested in knowing if there is any correlation between frequency of mows and time-period of mowing because it was speculated that mowing frequently may cause effects similar to prolonged mowing. So our last question is; (d) does frequent mowing speed up the process leading to long-term changes in species composition?

Methods

Study site and plot layout

The study site is located 16 km west of Stillwater in the Payne County, north central Oklahoma, USA, close to the Veterinary Medical Ranch (VMR) owned by Oklahoma State University. The site is a pasture with a moderately fertile soil of Graniola Lucien complex with a history of horse (*Equus caballus*) grazing and hay-clipping (Thompson 2005). A total of 144 permanent plots of 1 m² were laid out in 12 rows and 12 columns. The plots were subjected to eight treatments; seven mowing treatments varying in frequency and seasonality and an unmown (control) treatment. However, mowed plots were necessarily a combination of both mowing season and mowing frequency. In other words, the mowing treatments were all combinations of March, June and September mows resulting annually in 3 single mows, 3 double mows and a single triple mow. A stratified random design was applied such that 18 blocks consisting of 8 plots each having similar pre-treatment diversity measures received the eight treatments at random (Thompson 2005). Buffer strips of 73.5cm were subjected to a similar treatment as the core area and mowed 53cm walkways were maintained for easy movement between plots.

Data Collection and Statistical Methods

Following Thompson (2005) data were collected during early May and late August for the first three years and for the years 2004 and 2005 data were collected only annually during early May. All the species in the 1m² quadrat were listed and their abundance measured by visual estimation. Species abundances were assigned to one of following categories: rare, <1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75% or 75-

100%. All together, data for the years 1997, 1998, 1999, 2004 and 2005 were available through the 9 years of mowing experiment.

The differences in mean species richness values among the different treatments were analyzed by Analysis of Variance (ANOVA) using the statistical software, SPSS (version 12). In order to analyze the effects of frequency of mow, season of mow and time-period of mowing on species composition we used the ordination method of partial redundancy analysis (p-RDA). An array of p-RDA's were performed with various sets of environmental variables and covariables either in the presence or absence of control plots to analyze the effects of frequency, season and time-period of mowing on species composition (Table 1). The effect of season of mowing were studied by first considering all single season mows as environmental variables and then in a second p-RDA by specifying all pair wise combinations of the seasons mowed as environmental variable. The effect of time-period of mowing was studied by using years of sampling as environmental variable. Variables that compete with the designated environmental variable while determining latter's effects on species composition were treated as covariables. In a p-RDA the individual effects of two competing groups of environmental variables can be understood by factoring out or removing the effect of one set of variables by treating them as covariables (Borcard et al. 1992). This allows us to determine the independent effects of timing and frequency of mowing. Similarly, to find correlation between mowing frequency and time-period of mowing a combination of RDA and p-RDA were applied; first the total effects of both mowing frequency and time-period of mowing together on species composition is analyzed by RDA. For all the ordination analyses mid-values of cover classes were used to estimate species abundance

and the consequent change in composition. In a p-RDA, species composition is explained as a linear combination of a set of environmental variables after factoring out the effects of covariables (Lepš & Šmilauer 2003). The p-RDA was chosen because the data are nearly homogenous spread over a short environmental gradient and the environmental variables are categorical (ter Braak & Prentice 1988). All ordination analyses were done using CANOCO for Windows (version 4.5) software and CanoDraw software from the same package was used to create the species-environment biplots (ter Braak & Šmilauer 2002). In all the redundancy analyses, the canonical axes explaining the observed variation in species composition were tested for significance using Monte Carlo permutation tests.

Results

Effects on species richness

From the ANOVA results it is evident that for all years, except the first year of sampling mowing enhanced species richness ($P < 0.05$). However, among the different frequencies of mowing there was no significant difference in species richness, only a slight monotonic increase with frequency (Fig. 1). Similar results were obtained when March, June and September mowing were subjected to ANOVA; the seasons of mow also had no significant effect on species richness, but there was a slight increase in richness from early spring mows in March to late summer mows in September. It was also apparent from the species richness pattern for the entire mowing period that richness peaked at an intermediate time during the year 1999 and then gradually decreased (Fig. 1). In summary, mowing enhanced species richness; however, there was no specific outcome associated with frequency and season of mowing.

Effects on species composition

In the p-RDA testing the effects of all mowing treatments in the presence of control plots, the first axis shows that control plots are significantly different from mowed plots while the second axis of the biplot suggests that early mowing differ from late mowing significantly (Fig. 2a). While in a similar analysis with control plots removed, the first axis shows significant difference between early season mowing and late season mowing on species composition (Fig. 2b.). p-RDA studying the effects of mowing frequency showed no significant results when control plots were removed from the analysis suggesting that frequency per se has no significant effects on species composition. In p-RDA excluding control plots with year of sampling as environmental variable and all other mowing treatments as covariable showed significant results (Fig. 3). In this case, the first axis of the biplot suggests significant difference between early years of sampling and late years of sampling, however the second axis also suggests of difference between years 2004 and 2005 in the species composition associated with them. The results of the analyses of seasonal effects were highly significant for both single season mows and double season mows, and the biplots of the analyses showed a significant first axis that indicated that there is a significant difference between early season and late season mowing (Fig. 4a, b).

Testing for correlation between time-period of mowing and frequency of mowing, we found them to be uncorrelated. Out of a total 11.7 % variation explained jointly by mowing frequency and year of sampling, 10.09 % was explained by year of sampling.

Discussion

Effects on species richness

The observed richness enhancing effect of mowing was in accordance with previous mowing studies (Zobel et al. 1996; Collins et al. 1998; Maron & Jefferies 2003; Gusewell & Le Nédic 2004; Antonsen & Olsson 2005). The enhancement is mostly likely the result of litter removal (Maron & Jefferies 2003) and canopy opening (Zobel et al. 1996; Maron & Jefferies 2003). Both these alterations to vegetation architecture enhance species richness by increasing availability of light (Lepš 1999; Kotowski & van Diggelen 2004) and microsites for colonization (Stampfli & Zeiter 1999; Zobel et al. 2000). Though we do not have any statistical proof, it is quite apparent from the species composition in the unmown control plots that dominance by a few vigorously growing species (see Zobel et al. 1996; Huhta et al. 2001) has competitively excluded the weaker species and lowered the species richness (Grime 1973; Huston 1979, 1994). Studies have also proposed and shown that higher species richness from disturbances could result from higher propagule availability as seed rain and soil seed bank (Primack & Miao 1992; Kotanen 1996; Tilman 1997; Stampfli & Zeiter 1999). However, we do not have any evidence that mowed plots received more propagules (see Goldberg 1987; Kotanen 1996). It can be summarized that mowing created patches of increased variability in resource availability which allows species with different colonizing and competitive abilities to coexist.

The nearly invariant effect of increasing frequency of mowing during any given year is in conflict with the IDH. There are several potential explanations for the observed monotonic increase in richness with frequency; the simplest possible explanation is that

the different treatments are not really different with respect to their resource altering strengths (Armesto & Pickett 1985). Moreover, even if the treatments did alter the resource conditions uniquely, the species pool of the “response species” (in this case the light demanding species) may be a limiting factor (Zobel 1997). Partial mortality induced by mowing and ability of plants to resprout may also influence the degree of response to different mowing frequencies (Grace 1999). However, it is of interest to note that for the entire time-period of the mowing experiment, the five years of data show an intermediate peaking of richness during the sampling year 1999 and this is in lines with the IDH. Response of community to mowing is slow, with a gradual increase in species tolerant to mowing and parallel slow decrease in species sensitive to mowing. At an intermediate time scale irrespective of the mowing frequency maximal species richness is attained when both mowing sensitive and mowing tolerant species are equally abundant. Shea et al. (2004) resonate this in principle by stating that disturbance need to scale relative to the generation time of organisms in the community such that the intermediate scale lies between shortest lived species and long lived dominant species. In theory, this implies for a grassland community comprising annuals at one end and perennials at the opposite end, mowing annually sets the lower limit while mowing once in a few years set the upper limit and between these upper and lower bounds should ideally exist the intermediate frequency level.

Species richness response to different seasons of mowing is similar to mowing frequency, a slight monotonic increase with maximum richness in September mow. Based on phenology, prairie plants are divided into two broad categories: early (spring) flowering and late (summer) flowering species (Rabinowitz & Rapp 1980; Howe 1994).

Further, Howe (1994) has shown that if tallgrass prairie species are categorized into phenological groups of early, mid and late flowering seasons the distribution of species is nearly equal. Therefore, it is reasonable to assume that the nearly similar richness found in our study during different seasons of mowing suggests of the equal availability of species.

Effects on species composition

Species compositional changes affected by various combinations of the mowing treatments revealed a more complete picture of how season, frequency of mows and year of mowing affect species composition. In all the p-RDA carried out, removal of control plots did not alter the statistical significance of the results, except when mowing frequency was used as an environmental variable. In analyses that include control plots the first axis suggests that most of the variation in species response is explained by mowing versus non-mowing treatment. This strong effect of control on species composition is because tall forbs like *Monarda fistulosa* and *Euphorbia marginata* and grasses with large blades and canopies like *Elymus canadensis* and *Andropogon gerardii* dominate control plots. The control plots also recorded occasional presence of shrubby species like *Symphoricarpos orbiculatus* and *Ulmus sp.* The presence of these species suggests that under unmown conditions tall forbs and ligneous shrubs may slowly replace most other species and eventually dominate these undisturbed conditions. Similar findings have been reported in previous studies where cessation of disturbance or undisturbed conditions causes invasion and spread of woody species (Zobel et al. 1996; Collins et al. 1998; Gusewell & Le Nédic 2004). In comparison to the control plots, the mown plots selects for a very different species composition, here short statured species

like, *Linum sulcatum* and *Erigeron strigosus* are found in high abundance. The selective advantage of short-statured plants with prostrate habit has been documented in other similar studies (Lepš 1999; Antonsen & Olsson 2005). However, few woody and tall forbs like *Amphiachyris dracunculoides*, *Hedoma hispidum* and *Solidago missouriensis* were observed in low abundance in the mown plots, this perhaps is indicative of the ineffectiveness of mowing in completely annihilating certain species. Clark and Wilson (2001) have also reported that mowing is often not as effective as fire or hand removal in controlling the spread of certain woody species as mowing left basal stems and underground perennating structures intact.

The season of mowing also show some characteristic change in species composition. Mowing during early season (March or June and March-June) favored late season grasses like *Andropogon gerardii*, *Bothriochloa ischaemum* and *Sorghastrum nutans*, however the effects of late season mowing in September did not show any such strong preference for early season species with *Sisyrinchium campestre* being the only exception. The results suggest that seasonality of mowing gives a competitive advantage to the species flowering and seeding outside the season of mowing. Similar results have been reported previously by seasonality of fire and mowing on species composition (Hover & Bragg 1981; Howe 1994). It has also been proposed that predominance of late-season plants in remnants of tallgrass prairie is largely due to the current management practice of dormant season burning (Howe 1994). The effect of mowing frequency failed to show any significant results in the absence of control plots.

The effect of time period of mowing is well shown by the biplot in that the early years of sampling differed from later years of sampling. Species like *Bothriochloa*

saccharoides and *Nothoscordum bivalve* are abundant during the early years (1998 and 1999). In the recent years (2004 and 2005) species like *Sisyrinchium campestre*, *Bouteloua curtipendula*, *Schizachyrium scoparium* and exotic *Bothriochloa ischaemum* are found in high abundances. In a 20 year long-term study on calcareous fens, species compositional changes were more or less clear after first four years of mowing with little changes thereafter (Güsewell et al. 1998). Another 15 year long study on the management of semi-natural grasslands reported a 5 year delay before the effects of abandonment were visible (Hanson & Fogelfors 2000). In this study, a shift in species composition was apparent by the 7th year of sampling but due to the absence of sampling during the 4th, 5th and 6th year it is uncertain if the shift had actually occurred earlier. However, the nature of the shift in species composition is not apparent from the analysis. Frequency and time-period of mowing was also found to have independent effects, suggesting that mowing 3 times a year did not as speculated speed up changes towards a species composition similar to mowing over long time periods.

In conclusion, the experimental study has shown that mowing alters both species richness and composition in a grassland community. The study also demonstrated that despite the initial positive effect of mowing on species richness, prolonged mowing might lead to a new steady state with mowing tolerant species increasing in abundance and species sensitive to mowing decreasing. Hence, mowing like other disturbances elicit mixed response from the various species in a community with some gaining in abundance while others are extirpated.

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Figures and Tables

	p- RDA	Environmental Variable	Covariable	Variable Excluded
1.	Treatments with control	All mowing treatments	Years of sampling	None
2.	Treatments without control	All mowing treatments	Years of sampling	Control
3.	Frequency of mowing	Frequencies of mow	Years of sampling	Control
4.	Year of sampling	Year of sampling	Treatments of mow	Control
5.	Season of mowing	Single mows of March, June and September	Years of sampling	All except March, June and Sept.
6.	Season of mowing	Double mows of March-June, June- Sept. and March-Sept.	Years of sampling	All except March-June, June-Sept. and March-Sept.

Table 1: Table shows the various p-RDA performed to study the effects of mowing on species composition. Depending on the analysis the environmental variable and covariables are selected. All together the following variables have been used in the analyses; mowing treatments – all possible combinations of March, June and September mows, frequency of mowing – single, double and triple mows, season of mowing – March, June and September or March-June, June-September and March-September mows and years of sampling – 1997, 1998, 1999, 2004 and 2005.

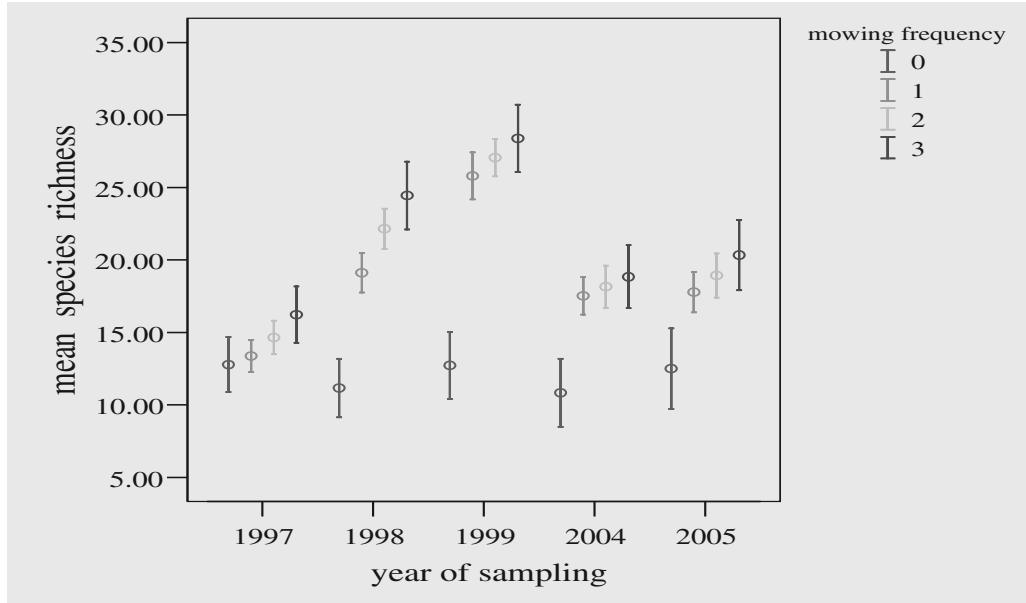


Figure1: Error bars showing the variation in mean species richness (at 95% C.I) for five sampling years across four different treatments (control - 0 , single mow per year - 1, double mow per year - 2 and triple mow per year – 3). The year 1997 shows no significant difference in species richness for all treatments, for all other years the control plots have significantly lower species richness than mown plots ($P < 0.05$).

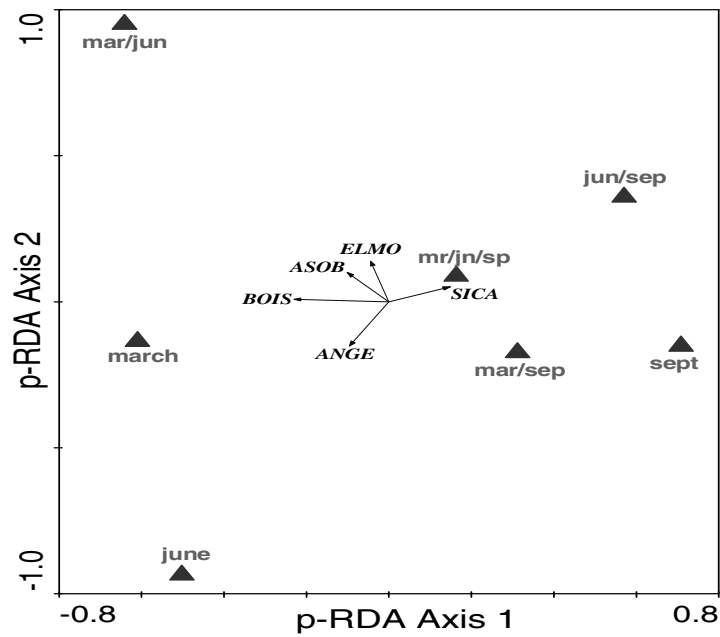
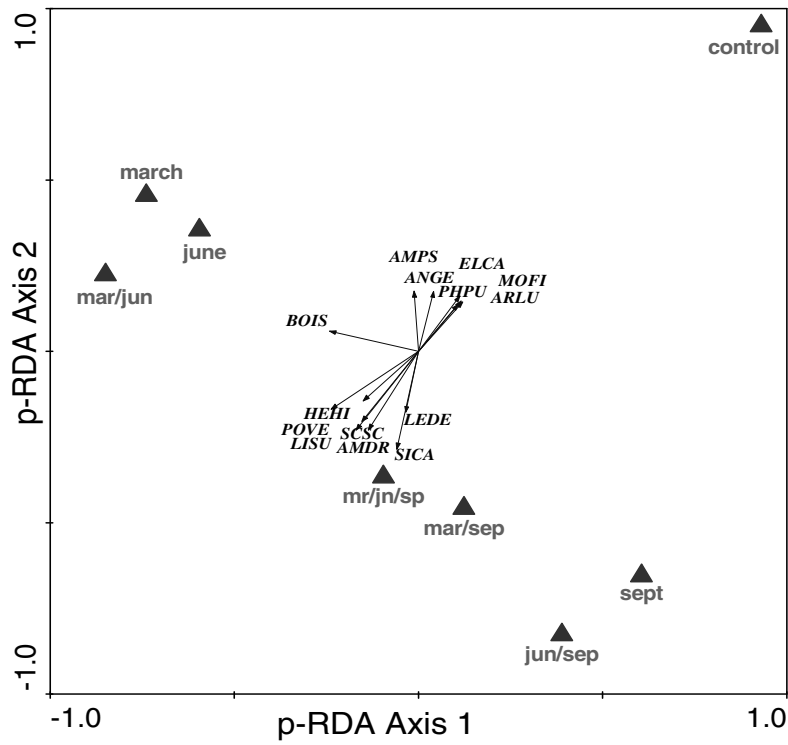


Figure 2 – a. RDA biplot shows the effects of all mowing treatments in the presence of control plots of on species composition. The RDA axis 1 indicates that the effect of control is significantly different from rest of the treatments ($P < 0.05$). b. RDA biplot

shows the effects of all mowing treatments in the presence of control plots of on species composition. The RDA axis 1 indicates that the effect of early season of mowing (March and June) is significantly different from late season effects of mowing (September) ($P < 0.05$). The species names are abbreviated in capital letters and the lengths of the arrows are in proportion to their covariance with axes (See Appendix 1 for species names in full).

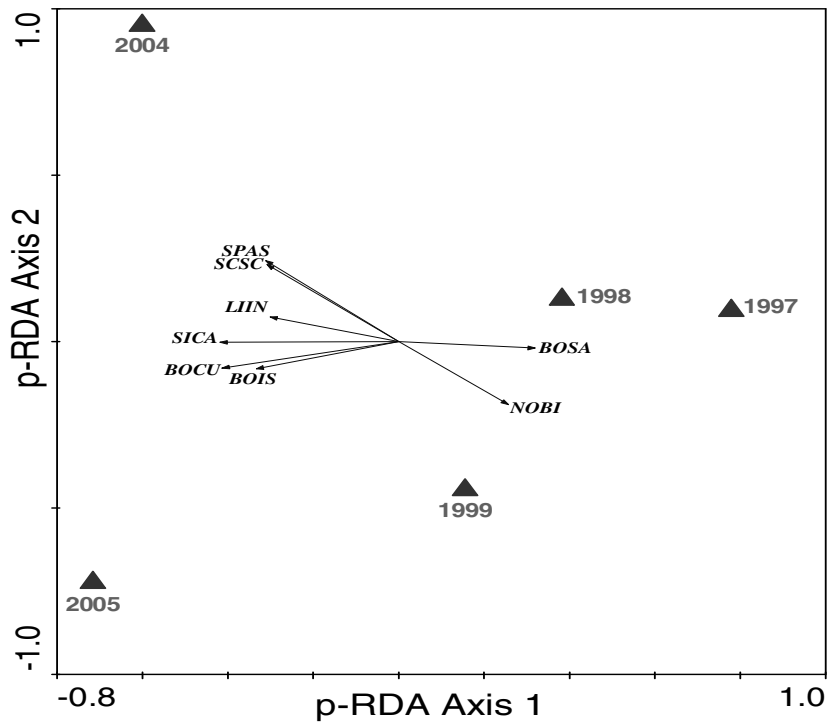


Figure 3: RDA biplot showing the effect of year of sampling on species composition. The first axis indicates there is a significant difference between early years of sampling and late years of sampling on species composition ($P < 0.05$). The species names are abbreviated in capital letters and the lengths of the arrows are in proportion to their covariance with axes (See Appendix 1 for species names in full).

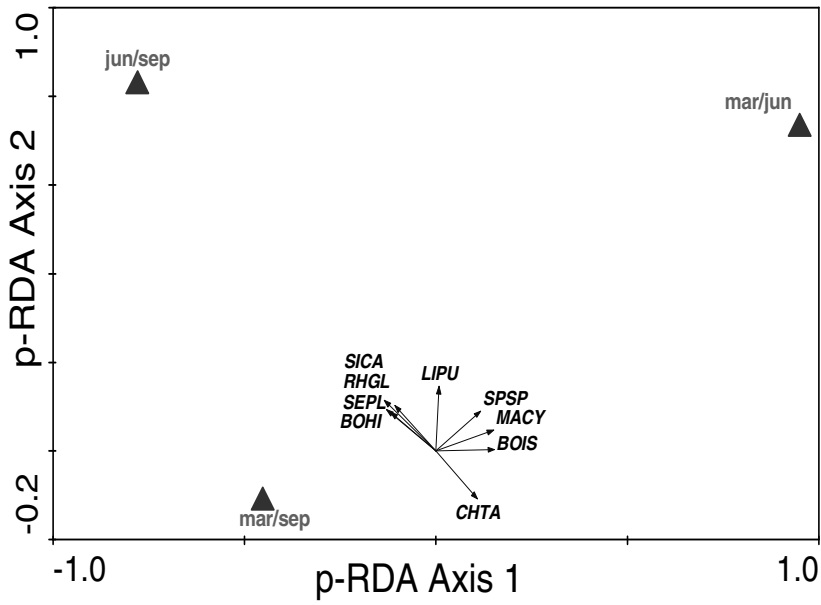
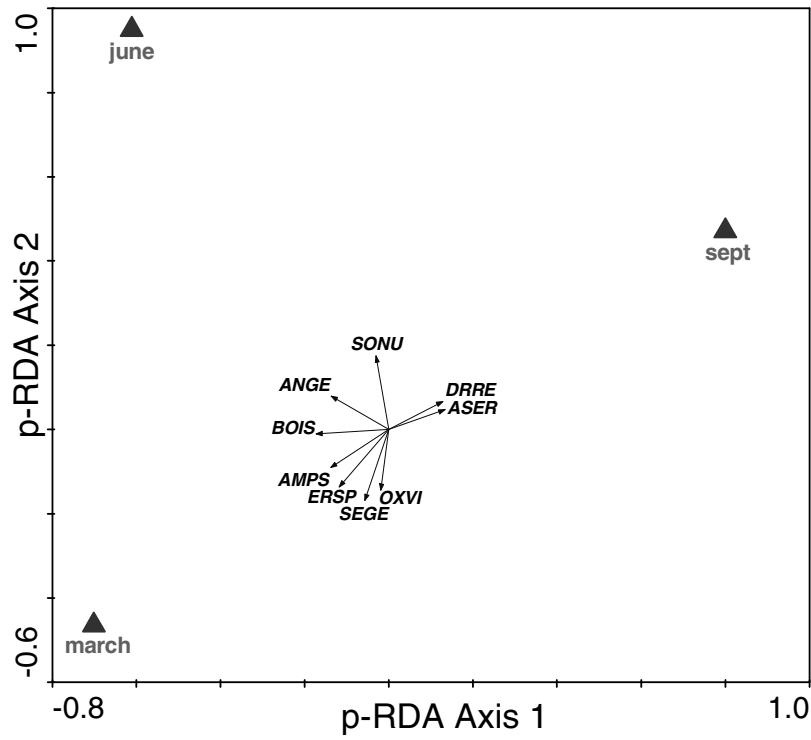


Figure 4 – a. Biplot shows the effects of season of mowing in the absence of control plots on species composition. The first axis indicates significant difference between early season of mowing and late season of mowing ($P < 0.05$). b. Biplot shows the effects seasonal double mows on species composition. The first axis suggests of significant difference between early season combination of March-June mows from late season combination of March September and June September mows ($P < 0.05$). The species names are abbreviated in capital letters and the lengths of the arrows are in proportion to their covariance with axes (See Appendix 1 for species names in full).

Appendix 1

Species Codes	Species Names
AMDR	<i>Amphiachyris dracunculoides</i>
AMPS	<i>Ambrosia psilostachya</i>
ANGE	<i>Andropogon gerardii</i>
ARLU	<i>Artemisia ludoviciana</i>
ASOB	<i>Aster oblongifolius</i>
ASER	<i>Aster ericoides</i>
BOCU	<i>Bouteloua curtipendula</i>
BOHI	<i>Bouteloua hirsuta</i>
BOIS	<i>Bothriochloa ischaemum</i>
BOSA	<i>Bothriochloa saccharoides</i>
CHTA	<i>Chaerophyllum tainturieri</i>
DRRE	<i>Draba reptans</i>
ELCA	<i>Elymus Canadensis</i>
ELMO	<i>Eleocharis montevidensis</i>
ERSP	<i>Eragrostis spectabilis</i>
ERST	<i>Erigeron strigosus</i>
HEHI	<i>Hedeoma hispidum</i>
LIIN	<i>Lithospermum incisum</i>
LIPU	<i>Liatris punctata</i>
MACY	<i>Manisuris cylindrica</i>
MOFI	<i>Monarda fistulosa</i>
NOBI	<i>Nothoscordum bivalve</i>
OXVI	<i>Oxalis violacea</i>
PHPU	<i>Physalis pumila</i>
POVE	<i>Polygala verticillata</i>
RHGL	<i>Rhus glabra</i>
SCSC	<i>Schizachyrium scoparium</i>

SEGE	<i>Setaria geniculata</i>
SEPL	<i>Senecio plattensis</i>
SICA	<i>Sisyrinchium campestre</i>
SONU	<i>Sorghastrum nutans</i>
SPAS	<i>Sporobolus asper</i>
SPSP	<i>Spiranthes sp.</i>

**The role of vegetation science in conserving the montane grasslands of
Western Ghats**

Introduction

The montane grasslands and adjacent evergreen tropical forests (locally called the shola-grasslands and shola-forests) form a distinctive vegetation mosaic on the Western Ghats. The Western Ghats is a mountain range that runs north-south parallel to the western coastline of the Indian peninsula from 8° N to 22° N. This range is classified as a distinct biogeographic zone of India (Rodgers and Panwar 1988) and a biodiversity hot-spot along with Sri Lanka (Myers et al. 2000). The montane grasslands and adjacent forests face several threats largely due to increasing anthropogenic activities. Once widespread across the high altitudes of Western Ghats, the grasslands are now highly fragmented and restricted to approximately 400 km² (Karunakaran et al. 1998). Unlike the adjacent forests, the grasslands have received meager attention from biologists. However, the sharp decline in the population of an endemic wild goat, the Nilgiri Tahr (*Hemitragus hylocrius*), indicated the grasslands are in danger of being lost and in need of conservation.

Setting up preserves is the first step towards conservation, which needs to be backed up by active ecological research at various levels: population, community, and ecosystem (Soulé and Kohm 1989; Soulé 1991). In this respect, *ad-hoc* preserves and sanctuaries have been established to save the Tahr and its habitat. However, research on these grasslands is highly scattered. In this review, I bring together the sporadic works and evaluate the ecological understanding gained from them. For the most part, I shall focus on research done at the community level. I address two primary questions:

1) How much do we know about the ecology of the montane grassland community of Western Ghats? 2) How far does current understanding help in conserving the montane-grasslands?

Geography, Physical Environment and Paleohistory

The montane grasslands are located on the high plateau (> 1500 m) of Nilgiri, Palni and Anamalai Hills. The montane grasslands cover the tops of hills, while the valleys of these hills contain forests with stunted evergreen trees (Ranganathan 1938; Meher-Homji 1965; Karunakaran et al. 1998). The presence of these ecologically and physiognomically different communities makes the mosaic a unique landscape of interest to ecologists (Ranganathan 1938; Bor 1938; Meher-Homji 1968). Most works that tried to resolve the apparent paradox provided two main solutions: climatic effects (Ranganathan 1938; Meher-Homji 1965, 1967), and fire (Bor 1938; Gupta 1960, Chandrashekharan 1962; Noble 1967) and to this day there is no consensus among biologists (Karunakaran et al. 2000).

The climate is often referred to as '*temperate*' because of the relatively low mean annual temperatures compared to the low lying plains. The region is characterized by much greater diurnal variation of temperature than seasonal variation. (Meher-Homji 1967). The diurnal difference in temperatures could be as high as 12° C during winter (Ranganathan 1938; Meher-Homji 1965, 1967). Similar temperature conditions are also found in tropical montane regions of Central and South America, East Africa, Hawaii and Malaysia (Sarmiento 1986). However, the higher precipitation and low average altitude of Western Ghat peaks causes climate to differ dramatically from these tropical montane

regions. Most of the precipitation is received from the seasonal monsoon winds: particularly, the south west monsoon between April and September. The precipitation is highly variable across the mountain range, decreasing from west to east, and often as high as 7000 mm. The orographic effect of the mountains causes most of the monsoon rains to fall along the western slopes of the Western Ghats, while the eastern slopes depend on cyclonic storms from the north east monsoon.

The soil of these grasslands is derived from parent rocks which are gneiss, charnockites and schists (Meher-Homji 1967; Sukumar et al. 1993), and the soil is known to be deficient in calcium (Ranganathan 1938). Studies along the forest-grassland edge found a sharp soil moisture gradient with moisture rich soil in forests and relatively dry soil within grasslands (Jose et al. 1994, 1996). This was observed by earlier workers, who considered the grasslands and forests to be edaphic climaxes caused by differences in soil moisture (Ranganathan 1938; Gupta 1960).

Studies are scant on the paleohistory of montane grasslands and the available information appears to conflict. In a pollen analysis of a bog in Nilgiris, the dominant community throughout the quaternary period was grassland with occasional declines and concomitant increase in pteridophytes, the latter indicating moist conditions (Menon 1967). A study within the shrub-savanna zone in Nilgiris revealed the presence of charcoal, indicating forest that was repeatedly destroyed by fire (Meher-Homji 1967). More recent radiocarbon studies reveal a fluctuating climatic history of the Nilgiris; with arid conditions dominated by C₄ plants around 16kyrBP, an interim wet period dominated by woody C₃ plants at 12kyrBP and the present return of dry conditions (Sukumar et al. 1993). This study also revealed a strong association between mean annual temperatures

and monsoon; this link could have serious implications for the grasslands in present times of global warming (Sukumar et al. 1993). Overall, paleohistorical studies show that both grasslands and forests were present prior to human habitation on these mountains and the vegetation type is determined largely by fluctuations in monsoon rain. However, human presence and actions since the Paleolithic times are also expected to have influenced the montane vegetation as seen today (Chandaran 1997), as will be discussed later.

Species Richness and Composition

An exhaustive inventory of the plant species of the montane grasslands is far from complete. However, with as many as 17% endemic species, the montane grasslands are unequivocally a conservation priority. This high degree of endemism associated is thought to be the consequence of island-like conditions of mountaintops. 308 vascular plant species belonging to 59 families and 178 genera have been collected so far from the 96 sq km Eravikulam National Park (ENP) (Karunakaran et al. 1998). This was 108 species more than the previous checklist (Shetty and Vivekanandan 1971), and the current numbers is considered an underestimate (Karunakaran et al. 1998). However, since there is no specific mention of the area covered during these collections, the number fails to provide any insight into the richness of these montane grasslands. Habitat type and disturbance influence species richness, as was evident from the impoverished cattle grazed sites and species rich forest-grassland edge habitats (Karunakaran et al. 1998).

Early works describe species composition of these grasslands by the most ubiquitous plant species (Ranganathan 1938; Gupta 1960; Meher-Homji 1965). Several

botanists have independently classified the shola-grasslands into different associations based on dominance of certain species (Table 1). A study on the ecology of Niligiri Tahr describes the Tahr habitat as an association of *Eulalia phaeothrix* and *Dicanthium polytychum* (Rice 1988). More recently, ordination showed that the grasslands are variable in species composition and this variability is due to differences in soil factors (Karunakaran et al. 1998; Rawat et al. 2000). Ordination of the montane grasslands of Sri Lanka also suggests that difference in soil types, altitude and precipitation determine the community type (Pemadasa and Mueller-Dombois 1979; Pemadasa 1990). However, floristic comparisons show that montane grasslands of Western Ghats are more similar to Western Himalayan region than to the tropical montane grasslands of Sri Lanka (Karunakaran et al. 1998). These results parallel a recent study on the molecular phylogeny of herpetofauna of Western Ghats and Sri Lanka (Bossuyt et al. 2005). All these suggest minimal exchange of organisms between the two land masses and imply that they should not be considered a single biogeographic unit (Bossuyt et al. 2005).

Though species richness, diversity indices, classification and ordination have been attempted, they only provide a rudimentary understanding of the community. This is largely because of the absence of empirical patterns of species diversity like species-area, species-productivity and species-disturbance relationships and their generalizations. From the perspective of a multi-species community, they allow better understanding of species interactions and coexistence. For example; investigating species-area relationship could reveal the role of habitat diversity or the island like conditions of mountain tops in maintaining species diversity (Kohn and Walsh 1994; Rosenzweig 1995). Also, species-

area relationships have been useful in determining reserve area and design (Gitay 1991) and in estimating extinctions following habitat loss (Pimm et al. 1995).

Most vegetation dynamics in a plant community are the result of the complex interplay between productivity and disturbance (Grime 1973; Huston 1979; Proulx and Mazumder 1998). The hump shaped biomass-diversity relationship and the intermediate disturbance hypothesis (Connell 1978; Huston 1979) are two well known theoretical generalizations of how productivity and disturbance influence species richness. The role of productivity is well exemplified by oligotrophic species rich meadows of Europe, in these meadows there is well established negative relationship between species richness and productivity. Increase in productivity of these grasslands through agricultural run offs leads to increase in stem density and competition for light which decrease species richness (Willems and Nieuwstadt 1996; Lepš 1999). Disturbances like grazing reverse this trend by removing the competitively superior species and allowing the weaker species to establish under improved availability of light. Productivity not only determines species richness by limiting resource availability in unproductive conditions or through increased inter-specific competition for resources in highly productive conditions, but also determines the rate of succession in grasslands. Such grasslands are often dependent on disturbances for preventing invasion by shrubby species (Chins et al 1998; Collins 2000). Disturbances are the main source of spatial variability, which is essential for coexistence among species in a community. Several studies on grasslands and other communities have highlighted the role played by both biotic and abiotic disturbances in maintaining spatial variability (see review by Pickett 1980; Sousa 1984). Not surprisingly, knowledge of local disturbance regimes is a constant subject of research and

application in grassland conservation. For example; fire in tallgrass prairie (Collins 2000), gophers in serpentine grasslands (Hobbs and Mooney 1995) and grazing in prairie and Serengeti grasslands (McNaughton 1985; Knapp et al. 1999).

Even descriptions of community structure as described by patterns such as relative species abundance and species rank diagrams are absent from studies on shola-grasslands. These descriptors of community structure may not have direct applications *per se*; however they are fundamental for understanding any community. This is well highlighted by species rank diagram where the shape of line or curve reveals useful biological information about the community such as successional stage and effects of disturbance or pollution (May 1976). Similarly, the species abundance distribution pattern provides valuable insights into the structure of a community like the core-satellite hypothesis proposed to explain the abundance distribution pattern of prairie grassland species (Hanski 1998).

Succession and the Climax concept

There has been no long-term successional study of these grasslands and most works are limited to either determining or discussing the nature of climax. Not surprisingly, the forest-grassland mosaic triggered debate on the true successional status of grasslands and forests. Also, previous work attempted to identify the biotic and environmental factors behind the coexistence of grasslands and forests. Postulated factors include frost and grassland as the climactic climax (Meher-Homji 1965, 1967), fire / grazing and grassland as a sub-climax (Bor 1938; Noble 1967) and a more 'harmonious' climactic dual climax which lets both forest and grassland coexist as climax vegetations

(Ranganathan 1938). The debate becomes increasingly obscure in a flurry of terms like climatic climax, dual climax, biotic climax, pre-climax and so on. As evident from the terms, these works are heavily influenced by Clementsian idea of mono-climactic succession (Clements 1936).

In a phytogeographical study of the forest-grassland biome, Meher-Homji (1965, 1967) found that the shola-forest species show two principal floristic elements: tropical and extra-tropical (or temperate). The species of the shola interiors are mostly from tropical regions like the Western Ghats, Sri Lanka, or Indo-Malayan region, while the woody species along the fringes of the shola and in the adjacent open grasslands have subtropical to temperate origins (Meher-Homji 1967). Frost-induced stress is evoked to explain this distributional pattern. Ground frosts on the open grasslands prevent tropical species from establishing while the few that succeed in establishing are the temperate frost-adapted species (Meher-Homji 1967).

According to the fire hypothesis the grasslands are the consequence of frequent burnings from pastoral and agricultural activities by the early human settlers (Bor 1938). With no conclusive evidence for the frost hypothesis, the fire hypothesis has gained favor among ecologists and managers (Jose et al. 1996) with annual summer burning being the current management practice. Moreover, it needs to be stressed that there are hardly any studies done on the implications of the current management practice or effects of fire on the grassland community. In the only known experimental study investigating the effects of fire, winter burning was found most ideal as it checked the spread of woody species and also caused the least damage to endemics like *Strobilanthus kunthianesis*, but species richness was unaffected irrespective of the treatment (Karunakaran et al. 1998).

Long-term studies are a necessity to understand the succession of any community, and in their absence much of the current knowledge concerning succession remains mere speculations. Processes like site opening, species invasion or persistence and species interactions are known to be effected by disturbances (Pickett et al. 1987). Despite disturbances like frost, cattle grazing and fire being recognized on the montane-grasslands there are very few studies that examines the effects they have on succession consequently, the disturbance mediated processes of succession remain unrecognized. Further, it needs to be stressed that most ecologists see succession as a highly dynamics process of vegetation change with no easily predictable climax end points rather a set of potential relatively stable states that punctuate the dynamic cycle (Niering 1987). This dynamic view of succession is lacking in studies on shola-grasslands so far.

Human History and Impacts

The first human occupation of the Western Ghats region occurred around 12 000 years ago during the late Paleolithic times, and the first signs of agri-pastoralism occurred around 3000 – 5000 years ago (Chandran 1997). The earliest settlers and their origins remain unknown; speculations point towards southward migration of the Harappan people (Chandran 1997). Early works have touched upon the ethno-biology of the people of Nilgris and vicinity (Ranganathan 1938; Bor 1938; Noble 1967) with more detailed additions by Rajan et al. (2002) and a more comprehensive account by Hockings (1989). From these studies it is apparent that as many as seven different ethnic groups belong to the hills of Western Ghats. While almost nothing is known about their origins and early history, each ethnic group is identifiable as an occupational guild with a distinct culture

(Hockings 1989; Rajan 2002). Together they make a socio-economic system, like the caste system of the plains, exchanging goods and services (Hockings 1989).

Some people like the Badagas practiced slash and burn agriculture, while the pastoralist Todas tended buffaloes (*Bubalus bubalis*) which grazed these grasslands. Thus, anthropogenic modification has long been an important factor in these grasslands (Bor 1938; Noble 1965). Cultural practices and traditions often highlight the human-nature interactions, but such information is sparse concerning the grasslands of Western Ghats. Among the few such traditions that ethno-biographical studies document include worship of buffaloes (Hockings 1989; Rajan 2002) and the pastures by the pastoral Todas and the Badaga funeral practice of seeking absolution from a list of sins which are mostly crimes against nature (Hockings 1989).

The British rule abolished slash and burn cultivation and began large scale commercial plantations of cash crops like *Eucalyptus globulus*, *Acacia mearensii* and *Camellia sinensis* (tea) (Chandran 1997). The towns of Ooty and Kodaikanal on the Nilgiri and Palani hills respectively are the result of the trade and commerce initiated by the British. Thus, the British era saw the human impacts on the mountain system turn more exploitative and environmentally damaging. The monoculture plantations are now owned by Indian business houses and continue to have detrimental effects on the ecosystem (Guha and Gadgil 1995). Overall, the human history on the Western Ghats is long, with a trend of increasing human activity and consequent environmental harm. It needs to be stressed that most of the information in this section pertains to the mountain system as a whole, and it appears there are not many studies that specifically addresses the effects of plantations on the montane grasslands of Western Ghats.

Present Status and Conservation

As mentioned above, the scale and intensity of human activities has expanded from the local and less intensive effects of pastoral and agricultural activities to more intensive effects of commercial plantations. This increase has resulted in several threats to the biodiversity of Western Ghats. For example, Ooty and Kodaikanal have been transformed into summer holiday resorts with an unconstrained and booming tourism industry (Dharmalingam 2004), and the frequency of forest fires has increased threefold (Karunakaran et al.1998; Rawat et al.2000; Kondanpani 2004). Further, in post-globalization times there appears to be a strong influence of global market dynamics on local resource consumption patterns. In a study by Madhusudan (2005) the impact on local resource utilization like pastoral dung manure production was found to be heavily influenced by adjacent coffee plantations and fluctuations in global coffee prices.

Invasive and exotic species are also recognized as a serious threat to this high altitude ecosystem. Some, like *Acacia mearensii* and *Eucalyptus globulus* are the consequence of commercial plantation and afforestation drives (Dharmalingam 2004). Other invasives include *Lantana camara* and *Ageratina adenophora*; the reasons for their introduction are not known (Munniappan and Viraktamath 1993). Studies on *Eucalyptus globulus* have shown that they lower water table in the vicinity by absorbing large quantities of subsoil moisture (Samra et al. 2001; Dharmalingam 2004). As many as 30 grassland species have been categorized as endangered in a study restricted to ENP

(Karunakaran et al.1998). Another study on the hills of Palani found 70 rare or threatened species (Mathew 1999). However, autecological studies on any of these species are not known. Among the 30 species identified at ENP, Poaceae and Orchidaceae together comprise the majority and the major reason behind their endangered status is habitat loss and overexploitation by orchid collectors (Karunakaran et al.1998).

Another area of concern is the potential impact of global warming. Sukumar et al. (1995) predict that increase in mean annual temperatures would favor C₃ plants because increased CO₂ levels enhances the photosynthetic rates in C₃ plants and higher temperatures reduce ground frost enabling the C₃ forest plants to colonize grasslands. Given that the role of frosts in maintaining the forest-grassland mosaic is in dispute, this prediction remains mere speculation.

The Nilgiri Tahr demands a special mention because the shola-grasslands are both known through them and have gained conservation priority because of them. One of the most well studied species of the grasslands (Schaller 1970; Davidar 1978; Rice 1988, Mishra and Johnsingh 1998) and once widespread through most of shola-grasslands of the Nilgiri plateau (Davidar 1978) today they are reduced to few isolated populations within the protected preserves. Habitat loss, increase in poaching and other anthropogenic disturbances resulting from spread of human settlements are the main factors behind their dwindling numbers (Rice 1988; Mishra and Johnsingh 1998). While the role played by Nilgiri Tahr as a flagship species has benefited the conservation efforts, their ecological role within the grassland community is not known. Studies need to address the effects of grazing by Tahr on the grassland community composition and structure.

Discussion

From the above sections two conclusions can be drawn: 1) the montane grasslands of Western Ghats is a distinct and species-rich community with several endemic plant species; 2) as a community little is known about its structure, composition, working or seasonal dynamics. Studies that have significantly contributed to the present understanding are mostly from descriptive accounts, while observational studies with several replications and experimental studies involving manipulative treatments are few in number (Table 2). Moreover, among the few experimental works none have durations over two years, which precludes understanding long-term patterns. Not surprisingly, succession of these grasslands is poorly understood. The static description of communities based on the dominant species has prevailed in vegetation studies in India; this needs to be replaced by a more dynamic and quantitative approach, which views plant communities as mutable through space and time (Ganesh et al. 1997). Future studies also need to integrate the role of scale as most patterns in ecology are strongly intertwined with scale of the study (Levin 1992; Palmer and White 1994). This has been demonstrated for the grasslands of Rocky Mountain where the species richness in grazed and ungrazed conditions reflected the effect of scale (Stohlgren et al. 1999). Despite a long history of human presence, studies evaluating the effects of changes in anthropogenic influence mediated through changing socio-economic conditions and cultural values are almost absent except for Madhusudan (2005). As previously discussed, a wide variety of potential conservation threats have been identified: invasive species, forest fires, fragmentation, habitat loss and climate change. However, research addressing their effects on the montane grassland community is limited.

According to Pickett et al. (2004) understanding is the overarching goal of any science and ecological understanding is made possible by three tools: generalization, causal explanation and testing. With no generalizations or empirical patterns from studies on montane-grasslands, the present understanding of these communities are far from complete. Studies on nearly similar montane vegetation systems elsewhere have shown that disturbances like grazing; land use history and productivity are often crucial determinants of the community patterns and ecology (Diaz et al.1994; Petryna et al. 2002; Eskelinen and Virtanen 2005). Studies have also demonstrated that grassland animals like bison and gophers often affect community and population dynamics (Hobbs and Mooney 1985; Olf and Ritchie 1998; Knapp et al.1999). Similarly one can speculate the effects Nilgiri Tahr grazing may have on the shola-grasslands. On the same lines as grazing, frosts are known to play crucial role during seedling stage in limestone grasslands of Switzerland (Ryser 1991). It has been shown that frosts can prevent seedlings of several grassland species from establishing, but in the presence of neighboring ‘nurse’ plants the effect of frost is debilitated allowing species to establish amidst neighboring species (Ryser 1991).

In general research from grassland communities worldwide have shown that grasslands are highly dynamic systems where complex interactions among climatic variability, productivity, grazing, fires and topography are crucial to the understanding of these communities (Watkinson and Ormerod 2001). The global location of natural grasslands clearly suggests that climate with fairly long dry season is required; while in tropical region grasslands result often due to fire and grazing. However, none of these factors are exclusive to any region, for example, studies on the prairie grasslands have

revealed that fires and bison grazing strongly interacts with each other and over long periods of time with climate to affect the prairie community and ecosystem processes (Seastedt and Knapp 1993). Moreover, it has been recognized that it is not grazing per se, but intensities and varying spatial and seasonal effects of grazers that are responsible for maintaining a highly patchy environment which supports higher number of species. The bimodal species distribution pattern of prairie grassland species with numerous 'satellite' species that have a patchy distribution through space and time while the few 'core' species is relatively more permanent also indicates that grassland species dynamics are highly variable through space and time (Collins and Glenn 1991). Studies on chalk grasslands have also shown that in addition to grazing by sheep and productivity, topographical variables like slope and aspect are often crucial determiner of species richness and changes in species composition with higher species encountered on slopes facing equator (Bennie et al. 2006). Similarly, studies on Mediterranean grasslands of Spain have shown that slope and aspect are crucial determiners of species composition alone while species richness depended on grazing intensity (Amezaga et al. 2004). Overall, it can be summarized that to understand grassland communities a fair knowledge of various biotic and abiotic factors, how they mutually interact and influence vegetation dynamics through a varying scales of time and space is required.

To conclude, there are definitely several gaps in the current ecological understanding of montane grasslands of Western Ghats and this has a negative feedback on conservation efforts (Soulé and Kohm 1989). Understandably, conservation in India is criticized of being strongly "preservationist" in element (Saberwal 1996; Mishra and Rawat 1998). Identifying endangered species, communities or ecosystems followed by the creation of a

preserve or sanctuary summarizes the conservation approach in India. This has led to the creation of as many as 578 protected areas (national parks and sanctuaries) accounting for 4.7% of total land area and plans are drawn to increase the reserve numbers to 870 with an eventual cover of 5.74%. (Rodgers et al. 2002). It is implicit from these numbers that an increasing number of preserves will be small and discontinuous fragments of much larger and complete community or ecosystem. This strengthens the need for goal-oriented management of these small pockets of wilderness and such management depends heavily on the ecological knowledge of the species, communities or ecosystems they contain. The review establishes that there is good deal of work already done on these grasslands which provides the much needed base for building a more stronger and comprehensive understanding of these grasslands. This strongly bespeaks the need for vigorous and carefully planned long-term research in future for the conservation of these high altitude grasslands.

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Table 1. The classification of montane grasslands of Western Ghats into associations based on dominant species.

Author/s	Number of Associations	Climax Associations
Shankaranarayan (1958)	1	<i>Chrysopogon</i> sp.– <i>Themeda cymbaria</i>
Gupte et al. (1967)	1	<i>Dicanthium polytychum</i> - <i>Eulalia</i> sp.
Blasco (1970)	3	<i>Chrysopogon zeylanicus</i> - <i>Arundinella</i> sp. <i>Heteropogon contortus</i> - <i>Arundinella mesophylla</i> <i>Eulalia phaeothrix</i> - <i>Arundinella tuscatta</i>

Table 2. List of published works that have contributed significantly towards understanding the ecology of montane grasslands of Western Ghats.

Author/s	Study type	Focus of study
Ranganathan (1938)	Descriptive	Physical environment, climax
Bor (1938)	Descriptive	Fire, human impacts, climax
Meher-Homji (1965, 1967)	Phytogeography	Frost and climax
Gupte et al. (1967)	Observational	Species composition, succession
Rice (1988)	Observational	N. Tahr: behavior, ecology
Jose et al. (1996)	Observational	Forest-grassland edge, soil factors
Karunakaran et al. (1998)	Experimental	Species diversity, fire, conservation

VITA

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Thesis: Effects of mowing on tallgrass prairie grassland community over a nine year period and the ecology of the montane grasslands of the Western Ghats.

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Date: 28th May 2006

Institution: Oklahoma State University

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Title of Study: EFFECTS OF NINE YEARS OF MOWING ON TALLGRASS PRAIRIE
GRASSLAND COMMUNITY & REVIEW OF THE ECOLOGY OF MONTANE
GRASSLANDS OF THE WESTERN GHATS

Pages in study: 54

The thesis reported is a two chapter study on grassland their ecology, diversity and conservation primarily at the level of community. The first chapter is a study on the how mowing maintains small scale species richness of tall grass prairie grassland community. A grid of 144 1m² permanent plots was established at north central Oklahoma and a fixed mowing regime was maintained for a period of 9 years since 1996. The study demonstrated that species richness generally increased under mowing irrespective of the mowing treatment and mowing favored species with prostrate habits or perennials. Species composition showed significant changes under various combinations of mowing treatments, except for mowing frequency, season of mowing and time-period of mowing showed significant effects on species composition. Mowing over long time-periods showed a shift in species composition, while season of mowing appeared to favor species that seed outside mowed season.

The second chapter is a review on the montane-grasslands of Western Ghats, in South India which is located approximately 8° N of the equator. These tropical montane grasslands are famous for the endemic Nilgiri Tahr (*Hemitragus hylocrius*) that inhabits these grasslands. This review compiles and evaluates the literature to identify the conservation potential of these grasslands. Studies on these grasslands have suggested that these grasslands with adjacent forests are likely to be frost controlled. Long history of anthropogenic activities have been recorded on these grasslands, hence the role cattle grazing and pastoral burning are also likely to play key role in modulating these grassland systems. However, there is a lack of more comprehensive well planned long-term studies for the management of these grasslands.

Advisor's Approval: Michael W. Palmer