The Ecology of a South-Asian Tall-Grass Community

John F. Lehmkuhl
King Mahendra Trust/IIED
Grassland Ecology and Human Use Project
and
College of Forest Resources
University of Washington

The Ecology of a South-Asian
Tall-Grass Community

by

JOHN F. LEHMKUHL

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1989

Approved by____
(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree____________________________________

Date____

In presenting this dissertation in partial fulfillment of the requirements for the Doctoral degree at the University of Washington, I agree that the Library shall make copies freely available for inspection. I further agree that extensive copying of this dissertation is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for copying or reproduction of this dissertation may be referred to University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom the author has granted "the right to reproduce and sell (a) copies of the manuscript in microform and/or (b) printed copies of the manuscript made from microform."

Signature

Date Jan. 6, 1989

University of Washington

Abstract

THE ECOLOGY OF A SOUTH-ASIAN TALL-GRASS COMMUNITY

by John F. Lehmkuhl

Chairperson of the Supervisory Committee: Stephen D. West
Associate Professor
College of Forest Resources

Landscape dynamics, habitat succession, and grass production were studied for two years in a tall-grass and riverine forest mosaic in the Royal Chitwan National Park, Nepal. Ten grassland and three forest associations were identified on an edaphic and successional gradient. *Themeda arundinacea*, *Narenga porphorycoma*, *Saccharum bengalense*, *Saccharum spontaneum*, riverine forest, and *Shorea robusta* forest types were identified. A linear model of landscape dynamics showed that fluvial action controlled landscape organization. The landscape was not a "shifting mosaic" with constant properties; simulation showed *S. spontaneum* grassland area doubling over the next 50 years. Indirect gradient analysis suggested soil moisture, soil development, and fire as the underlying gradients of among-habitat organization. Succession was a complex function of life history and population processes, and increasing soil resources over time. Large mammals were important as ecosystem regulators.

Experiments were conducted in three grassland types to determine the effects of early (February) and late (May) dry season burning, and wildlife grazing on grass standing biomass and above-ground net primary production (ANPP). Grazing had a negative effect on *I.cylindrica* biomass, but not on *N.porphorycoma* biomass. Sites burned early had higher production, than late-burned or unburned sites. Increased production was attributed to high post-burn soil temperature. Annual above-ground grass production on sites burned early, the norm in Chitwan,

was 1.2 kg m^{-2} for *I. cylindrica*, 1.6 kg m^{-2} for *N. porphorycoma*, and 1.65 kg m^{-2} for *S. spontaneum*. Field studies showed domestic elephants each consuming 25 kg DW cut-fodder and 20 kg DW grazed forage daily. Humans legally harvested 11,132 t grass valued at NR 10 million (US $450,000). ANPP on a village pasture, or grazing lawn, was measured at 872 g m^{-2}, with 100% consumption by domestic livestock; ANPP inside an adjacent exclosure was 1410 g m^{-2}. A defoliation experiment indicated a negative nonlinear production response. Total grass production and consumption for the study area was projected with the landscape model assuming current conditions. Simulations projected little change in *I. cylindrica* biomass over the next 20 years, a 28% decrease in *N. porphorycoma* biomass, and a 15% increase in *S. spontaneum* biomass. Minimum consumption of ANPP by herbivores was 6% for the study area, with minimum consumption of 12% for *I. cylindrica*, 4% for *N. porphorycoma*, and 10% for *S. spontaneum*.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I was very fortunate in being able to return to Nepal and conduct the research that I had pondered ten years before while in the Peace Corps. I am most indebted to His Royal Highness Prince Gyanendra Bir Bikram Shah, Chairman of the King Mahendra Trust for Nature Conservation, for his support of nature conservation in Nepal, and the opportunity to work with the Trust and the Department of National Parks and Wildlife Conservation.

Dr. Hemanta R. Mishra, Member-Secretary of the King Mahendra Trust, was my "boss" during my Peace Corps days and during the research presented in this dissertation. He deserves special thanks for supporting me with the Trust's resources, encouraging me in my work, and for his dedication to nature conservation in Nepal. Mr. B.N. Upreti, Director-General of the Department of National Parks and Wildlife Conservation, also knew me from the Peace Corps days, and requires special mention for supporting the research and allowing me to work and live in Chitwan National Park.

Chief Warden Uday R. Sharma and Warden Ram Prith Yadav gave me support and cooperation in the field essential for successful completion of the research. The Ranger and other staff at Sauraha helped solve the day-to-day problems encountered in living and working at Sauraha.

Eric Dinerstein and the staff of the Smithsonian/Nepal Terai Ecology Project provided essential logistical help and advice in the field, and shared the life with me down in the jungle. I am indebted to Eric, and Chris Wemmer of the National Zoo's Conservation and Research Center, for supporting the project from the very beginning and encouraging cooperative research in Chitwan. Burt Levenson and Charles Hash, U.S. AID/Nepal, godfathered the project through its existence in Nepal, and gave me the institutional and logistical support to keep

the project moving. Burt and Amanda Levenson were more than generous with their hospitality in opening their home to me during my visits to Kathmandu.

Stephen Berwick, and the International Institute for Environment and Development, were the main financial sponsors of the project. Steve first thought of the idea of doing the grassland research in Nepal, had the stamina to see it begin, and provided the support to keep me going for two years. My first advisor at the University of Washington, Richard Taber, was instrumental in getting me to Nepal and guiding me at the University. Stephen West took over from Dr. Taber to guide me through completion of my graduate work. I thank my committee, Gordon Swartzman, Ray Huey, William Hatheway, and Linda Brubaker for their help.

I am indebted to the USDA Forest Service, Old-Growth Wildlife Habitat Relationships Project, for use of office space, computing equipment, and forbearance while I finished the dissertation during my first six months at the lab.

I could not have accomplished my goal without the help and companionship of my Project staff and many friends in Nepal. Maila Khumal was my personal assistant and housemate whom I came to rely on for help in the field, cooking my food, sharing his home and family, looking out for me the stranger, and companionship in the jungle. My other staff also kept me and the project going strong: Badri Tharu, Pashpat Tharu, and Sita Ram Khumal drove me through the jungle on our elephant, Man Kali; Ram Bahadur Lama put up with a troublesome jeep and a demanding boss to transport me by jungle and semi-paved highway roads; Tanka Bahadur Khumal helped me in the field with countless plots to count and cut grass. Mr. Rajesh Upreti was my botanist and advisor on things Nepali, who worked with the plant collection and identification. His family was a gracious host to me many times in Kathmandu, and made me feel as like one of their own. My friend

Surendra Mani Pathak kept me from feeling lonely with his good cheer, open table, and by singing and playing "ragas" to me. Other friends, Agni Kadka and Prakash Shrestha, were very kind in extending hospitality. The men of Jai Mangala village were my reliable part-time staff and neighbors.

Finally, I thank my parents for keeping faith in me and tolerating my unconventional way my life; and my wife, Katherine, who has been very loving and understanding.

CHAPTER I. GENERAL INTRODUCTION

The subjects of grasslands, large ungulates, and grass-ungulate relationships in the tropics usually conjures up the image of an East African plain teaming with wildebeest, zebra, antelope, and lions. One does not think of Nepal, or south Asia, as teeming with wildlife. Nevertheless, the region has had an amazingly diverse and abundant wildlife community in which ungulates and their predators have held a large role since Miocene times, 20 million years before present MYBP) (Wadia 1953; West 1984; Gaur 1987). In recent times, herds of ten thousand blackbuck (*Antilope cervicapra*) were reported in the Punjab by Jerdon (1874). Pollock and Thom (1900) described herds of thousands of barasingha (*Cervus duvauceli*) in Assam and Bhutan. "Incredible numbers" of "game species" were reported in the tall grass Terai jungles at the foot of the Himalayas near the beginning of the twentieth century (Inglis 1892). A fraction of these vast herds now are found only in national parks and reserves (Gee 1959; Schaller 1967).

Early accounts of the mammals generally were from the viewpoint of sportsmen or naturalists (e.g., Jerdon 1874; Blanford 1888; Lydekker 1924; Smythies 1942; Prater 1971). Few detailed ecological studies were done (Schaller 1967). More recent works have provided some detailed views of the large mammal behavioral and population ecology (Schaller 1967; McKay and Eisenberg 1974; Eisenberg and McKay 1976; Laurie 1978; Sunquist 1981), but much of the literature remains general or anecdotal (e.g. Proc. Symposium Animal Populations 1982; Mukherjee 1982).

Extensive taxonomic work has been done with the flora. Hooker contributed his monumental 7-volume work, *The Flora of British India* (1879-97). Numerous local floras were produced largely under the influence of a vigorous colonial forestry program (e.g. Beddome 1869-73, in Frodin 1984; Stewart and Brandis 1874; Brandis 1906). South Asians, and others, have continued to contribute to the plant taxonomy of the subcontinent (Babu 1977; Bor 1953, 1960; Kanjilal 1933; see Frodin 1984 for others). Plant ecological work has built on the early forestry work of Champion (1936; Champion and Seth 1968), and others, in the fields of forest ecology (Puri 1960; Bharucha 1975; Puri et. al. 1983), and in grassland ecology (Whyte 1957; Dabadghao and Shankarnarayan 1973; Yadava and Singh 1977; Misra 1979; among others). Grassland ecology research was strongly stimulated by support from the International Biological Program (Yadava and Singh 1977; Misra 1979).

My first experience with Nepal was as a Peace Corps volunteer with the Department of National Parks and Wildlife Conservation (DNPWC) during 1975-77. I had been unaware that the lowland Terai area of Nepal abounded with tropical "jungle" (a Nepali word for wild or undisturbed forest areas) with grasses 7 m high, and large animals like elephant (*Elephas maximus*), rhinoceros (*Rhinoceros unicornis*), and tiger (*Panthera tigris*). My curiosity was whetted by this experience, and I became interested in the relationships between the tall south Asian grasslands, fire, and large herbivores.

Research in Chitwan has been primarily on the large conspicuous mammals. Laurie (1979, 1982) studied rhinoceros from 1972 to 1975. Research conducted by the Smithsonian/Nepal Tiger Ecology Project from 1974 to 1983 concentrated on the tiger (Sunquist 1981; Tamang 1982; Smith 1984) and its prey, primarily axis (*Axis axis*) and hog deer (*Axis porcinus*) (Seidensticker 1976; Mishra 1982a; Tamang 1982; Dhungel 1985).

Very little research has been done on the plant communities that support this impressive vertebrate fauna. Laurie (1979) did a general survey of grasslands in conjunction with his rhinoceros research. Troth (1976) did some preliminary ecological studies of *Bombax ceiba* (Bombacaceae) that focused on the successional ecology of the species, and published a key to the common riverine forest shrubs (Troth and Nicolson 1976). Individual botanists have collected sporadically in the Chitwan District over the past 30 years, but no systematic collections have been made (see Hara *et. al.* 1978; for a complete list).

Literature on the organization of the grassland-riverine forest-sal (*Shorea robusta*) forest complex in north India and Nepal has been largely superficial (Bor 1960), inferred from casual observation and general treatments of similar grassland types (Puri 1960), or by general surveys (Dabadghao and Shankarnarayan 1973). Productivity research has been largely confined to northern India in dissimilar grassland types (Yadava and Singh 1977; Misra 1979).

It was obvious that research into the ecology of the riverine grasslands and forests was sorely needed for a complete understanding of the large mammal community and for park management. The potential was great for contributing as well to the basic understanding of grass-ungulate relationships in a system much different than the African grasslands where much research has already occurred.

I was given the opportunity to return to Nepal in 1985. The King Mahendra Trust for Nature Conservation (KMTNC), the DNPWC , and the International Institute for Environment and Development (IIED) developed a project to study the ecology of grasslands in Royal Chitwan National Park in conjunction with the Smithsonian/Nepal Terai Ecology Project (formerly the Tiger Project) research on rhinoceros ecology.

RESEARCH OBJECTIVES

The primary goals of the research were: 1) Investigate community organization at the landscape, among-habitats (beta), and within-habitat (alpha) levels, giving particular attention to the role of disturbance (fire, grazing, and fluvial action); 2) Determine the effects of fire and wildlife grazing on above-ground net primary productivity of the three major grassland types, *Imperata cylindrica*, mixed tall grass (MTG; primarily *Narenga porphorycoma*), and *Saccharum spontaneum*; and 3) Integrate landscape succession and production data into a simple simulation model to examine long-term trends in landscape and production dynamics, and test simple hypotheses.

A secondary goal was to acquire a base of knowledge on grassland ecology to explore at some later time the organization and ecology of the large-mammalian herbivore community. Implicit and fundamental to the work was the application of research findings to management. Specific hypotheses are presented in later chapters to address each of the three primary goals.

GENERAL STUDY AREA

Location

The Royal Chitwan National Park is located in the south-central Terai region of Nepal at longitude 84°, 20'E. and latitude 27°, 30' N. The Park occupies an area of 1040 km^2 in the Rapti valley of the Siwalik physiographic region (Mishra 1982a) (Fig. 1). The Churia and Someswar hills of the Siwalik Range form the southern boundary of the Park. The Rapti River forms the north boundary until its confluence with the Narayani River, which then forms the north and later west boundary down to the Indian border. Elevation ranges from 815 m on the crest of the Churia hills to 120 m along the Rapti River floodplain (Bolton 1975).

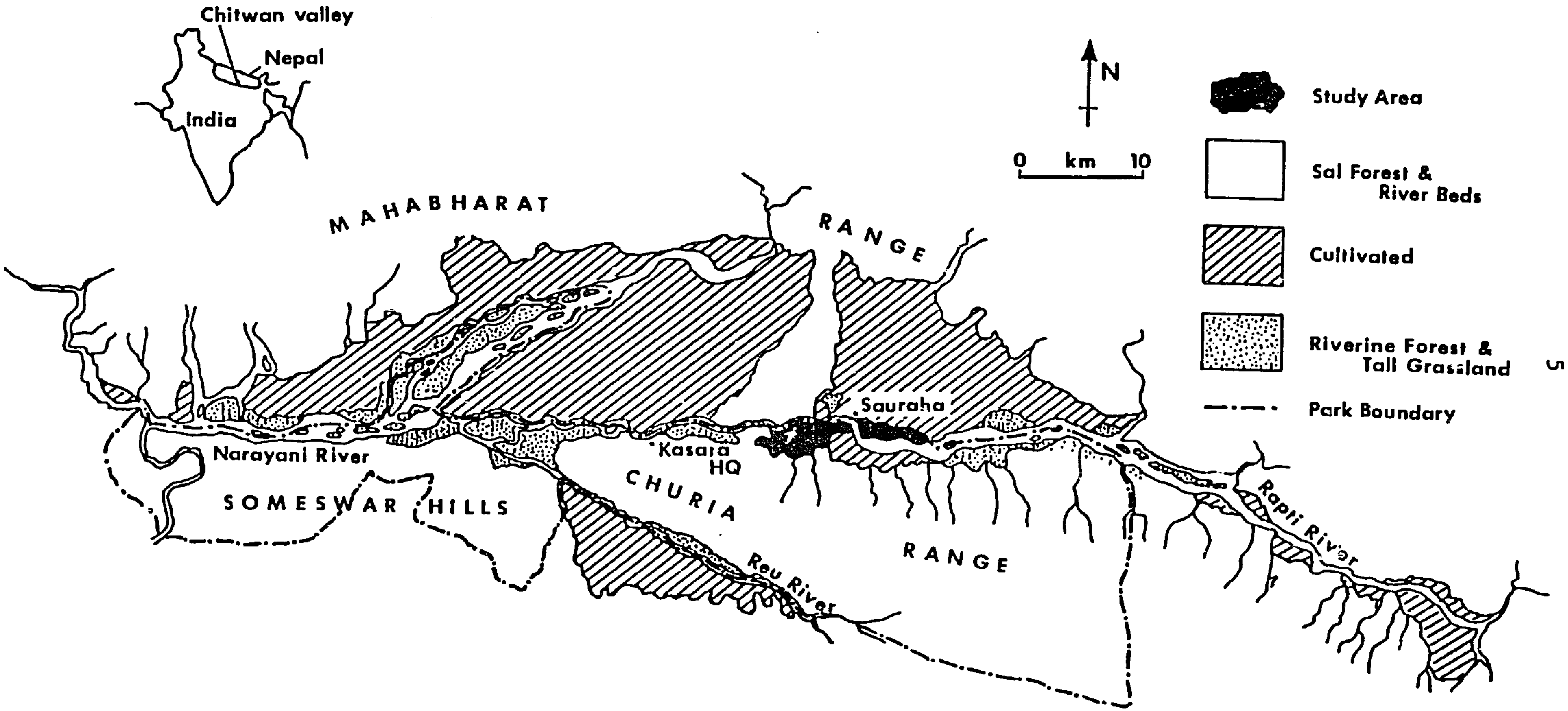

Fig. 1. Map of Chitwan valley, Nepal, showing location of Royal Chitwan National Park, research study area, general plant cover, and land use. (Base map modified from Laurie 1978).

Terrain ranges from the steep broken drainages of the Siwalik ranges to the level alluvial terraces ascending from the rivers on the valley floor.

Geology and Soils

The Chitwan Valley is a dun, or inner valley, within the Siwalik formation. Dun valleys are valleys whose outlets at some time were blocked by rapid tectonic uplift of the Siwalik range to the south of the main Himalayan foothills (Carson et al. 1986). Most dun valley soils reflect the lacustrine and fan-delta characteristics of the watershed draining into the basin during the late Tertiary period; however, the Chitwan dun has been much more affected by major river systems. The Narayani and Rapti rivers have markedly influenced the soils of the valley, almost eliminating the original basin deposits (Carson et. al. 1986). Soils are largely alluvial deposits left by shifting river courses (Fig. 2).

Park soils are representative of the Chitwan dun-valley types. Alluvial soils on recent terraces range from sand and course loams on new terraces to sandy and silty clay loam on older terraces (HMG 1968). Drainage is variable with the water table ranging seasonally from 0-2 m (Carson et. al. 1986). Older soils on fans, aprons and ancient river terraces are well drained sandy loam to loam. The water table seasonally ranges from 1-15 m. Hill soils are sandy loam to loamy rubble, with very stony surfaces less than 50 cm from bedrock. Surface drainage is very rapid, internal drainage is poor, and erosion is severe.

Climate

The Chitwan climate is subtropical and dominated by the summer monsoon. A dry season extends from about mid-October until pre-monsoon showers begin in late-April and May (Fig. 3). The monsoon typically begins around the first week of

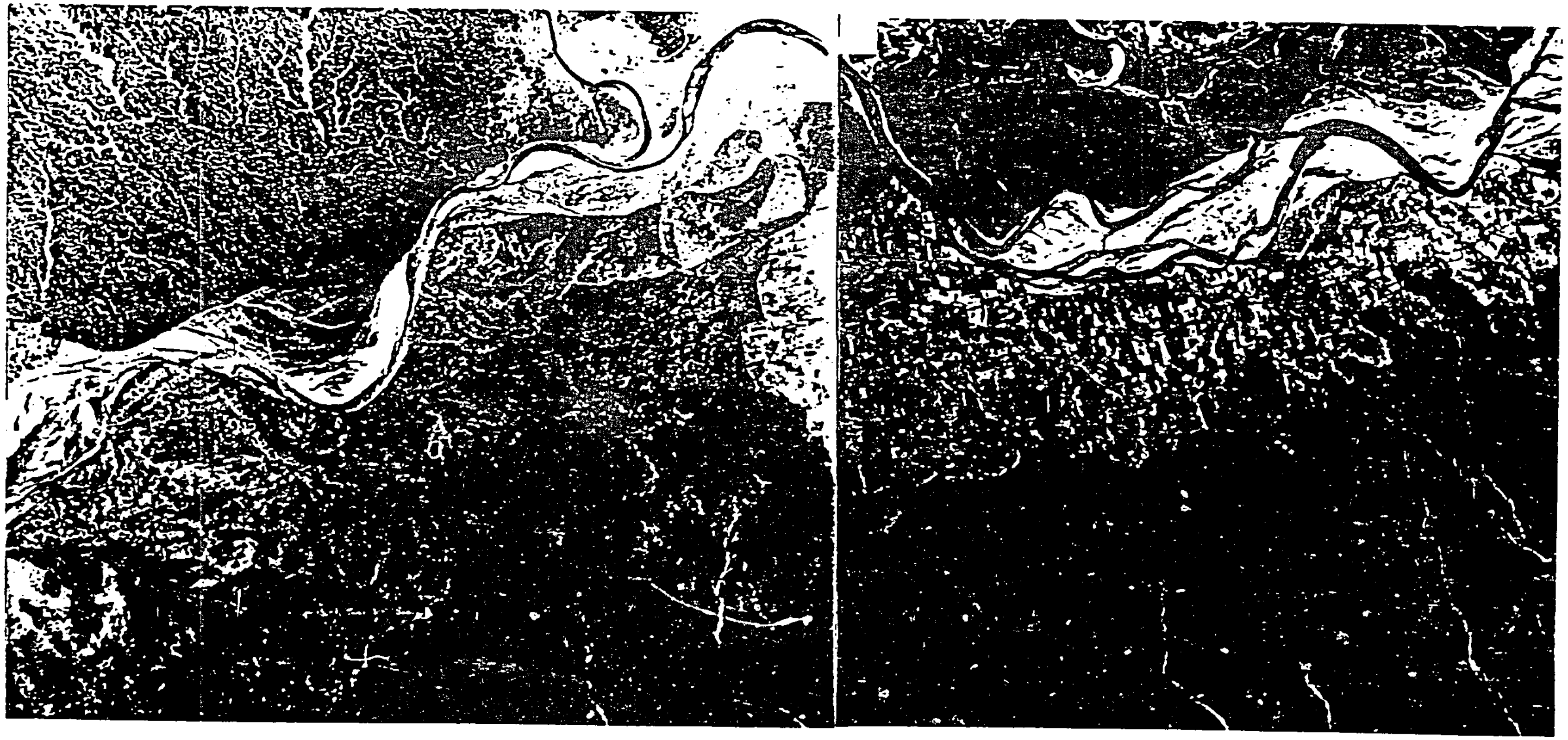

Fig. 2. Aerial photograph of research study area. Scale is 1:62,500, or 10 cm = 6.25 km. Landuse as mapped in Fig 1.

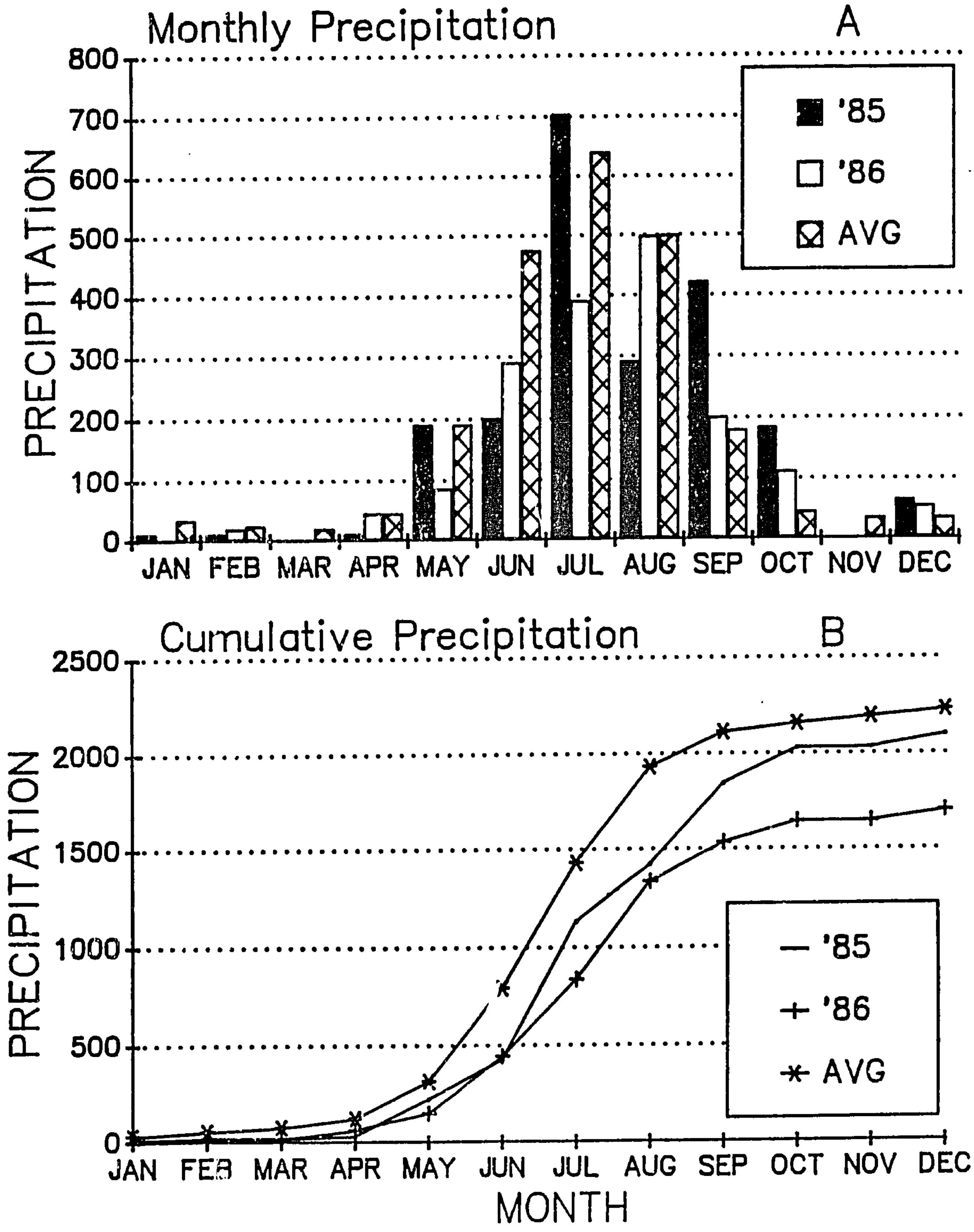

Fig. 3. Monthly precipitation for 1985 and 1986, and mean for 1958–1966 from Rampur Agricultural College, Chitwan District, Nepal. *A)* Monthly and average monthly precipitation; *B)* Cumulative precipitation.

June, peaks during July, and continues until late September and early October. Cumulative precipitation is typically over 200 cm, 80% falling during the June-September monsoon. Precipitation during the two years of the study averaged about 85% of the average from 1958-1966 as measured at the nearby Rampur Agricultural College.

Maximum temperature peaks during April and May (Fig. 4). The average maximum temperature during April is about 37°C, but temperatures can reach 45°C. Temperature declines very little until October, then declines rapidly to an average maximum low of 25°C during January. Minimum temperatures fall to an average 7°C low during January. Minimum temperature rises to a peak in July and August, during which the diurnal temperature range is smallest.

Humidity is high year round, often reaching 100% in the early morning during the monsoon, and during December-January when heavy fog covers the lower half of the valley for several hours after dawn (Laurie 1978). Warm dry winds from the west and southwest cause a rapid decrease in humidity from February through March, when humidity reaches a low of about 45%. Humidity and cloudy weather increases rapidly as the monsoon approaches with the change to easterly and southeasterly winds. Humidity peaks in July and remains fairly steady during the monsoon at about 85%, only declining slightly through January.

Vegetation

Sal (*Shorea robusta*; Dipterocarpaceae) forest covers about 70% of the Park (Bolton 1975), and is considered the "climatic" climax (Champion and Seth 1968; Puri 1960). Sal dominates the forest in nearly homogeneous stands 25-40 m tall, or sometimes in association with *Dillenia pentagyna* (Dilleniaceae), *Syzigium cumini* (Myrtaceae), *Lagerstroemia parviflora* (Lythraceae), *Phyllanthus emblica*

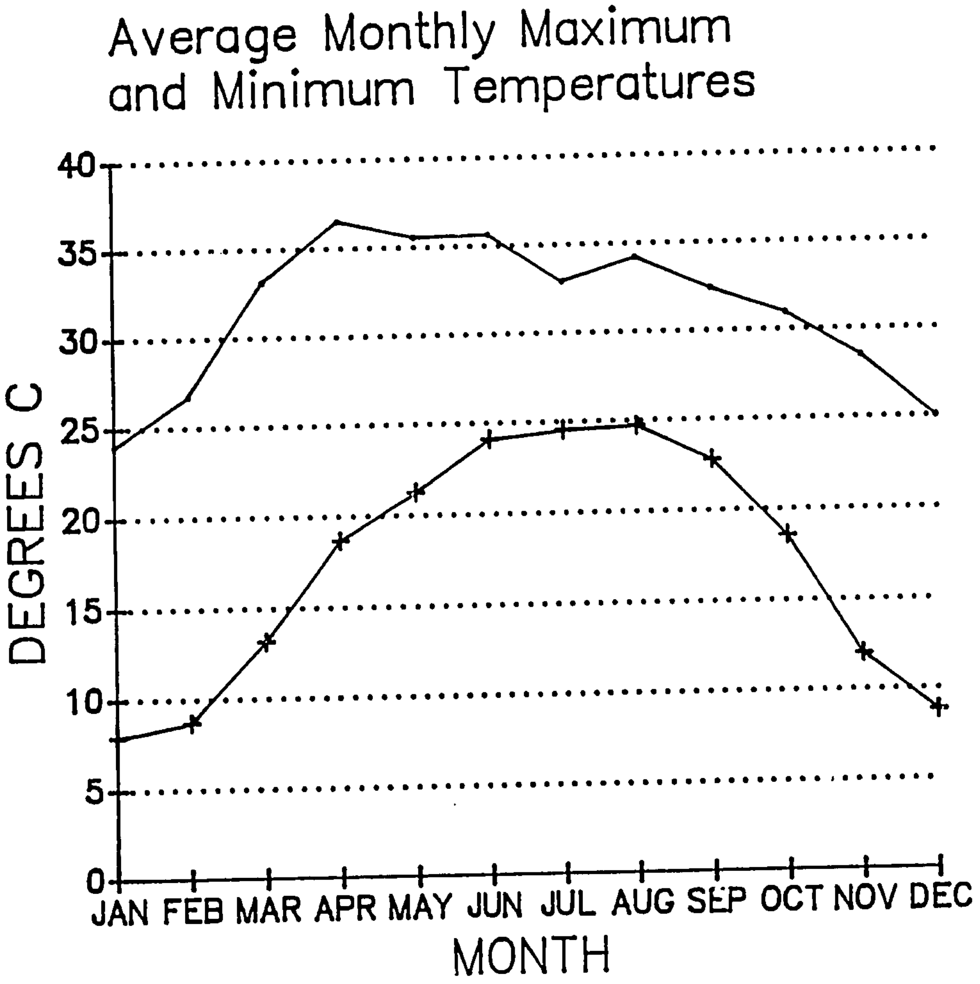

Fig. 4. Average monthly minimum and maximum daily temperatures for 1985 and 1986 at Rampur Agricultural College, Chitwan District, Nepal.

(Euphorbiaceae), and *Terminalia* spp. (Combretaceae). The understory ranges from a scanty shrub cover of *Clerodendron viscosum* (Verbenaceae) and *Pogostemon benghalensis* (Labiatae), among others, to tall (up to 7 m) *Themeda caudata, Narenga porphorycoma*, and *Arundinella nepalensis* grasses under the influence of fire. (Scientific names follow Hara et. al. 1978-82).

Deciduous riverine forest constitutes about 7% of the Park (Bolton 1975). Early successional stands are dominated by *Bombax ceiba* and *Trewia nudiflora* (Euphorbiaceae), with *Ehretia laevis* (Cordiaceae), *Litsea monopetala* (Lauraceae), and *Premna obtusifolia* (Verbenaceae). Late successional stands are characterized by remnant *Bombax* and *Trewia*, with a large evergreen component of *Persea* spp. (Lauraceae), *Syzigium* spp., *Mallotus philippinensis* (Euphorbiaceae), *Dysoxylum* sp. (Meliaceae), and *Ficus racemosa* (Moraceae).

Grasslands make up about 23% of the Park (Bolton 1975). *Saccharum, Narenga,* and *Themeda* species form tall (4-7 m) communities occur on hydric sites, and as savanna on more well-drained soils with *Bombax ceiba*, but also with *Xeromphis uliginosa* (Rubiaceae) and *Cleistocalyx operculata* (Myrtaceae). *Imperata cylindrica*, a short (1 m) grass, forms patchy monospecific stands on old agricultural sites abandoned since 1964, and is a sub-dominant in the tall-grass types (Dabadghao and Shankarnarayan 1973). *Saccharum spontaneum* forms tall, dense stands on recent floodplain alluvium.

Fauna

The Park supports an impressive diversity and biomass of large wildlife species. Ungulate biomass density in the grassland-riverine forest complex rivals that of some East African grasslands (Seidensticker 1976; Eisenberg and Seidensticker 1976). Primary grassland mammals are the tiger (Sunquist 1981), rhinoceros (Laurie 1978, 1982), and hog deer (Dhungel 1985). Axis deer is an "edge" species of the forest and grassland habitats (Mishra 1982a). Sambar (*Cervus unicolor*), muntjac (*Muntiacus muntjac*), and leopard (*Panthera pardis*) are primarily associated with forests (Mishra 1982a).

History

The Chitwan district was extensively cultivated prior to the first Nepalese war with the British Indians in 1816. Upon losing the war, the Nepalese removed settlements from Chitwan to create a malarious jungle barrier to further invasion from India (Oldfield 1880; Burkhill 1910). Oldfield noted in 1880 that "...the district about Chitwan is open and covered with long grass jungle, rather than forest, and is very much infested with rhinoceros..." and other game animals.

Through the late 19th and early 20th centuries, Chitwan remained a favorite and world-renowned hunting area for the then-ruling Rana family of hereditary Prime Ministers and their privileged guests (Fortescue 1906; Ellison 1925). The largest recorded bag of this century, taken during 1937-38, included 38 rhinoceros and 120 tigers (Smythies 1942). These grand hunts occurred about every 10-15 years, however, and the animals were taken from a relatively large area so it is likely that little permanent damage was done to populations (Caughley 1969).

The Rana regime fell and the monarchy was reinstated during the early 1950's. A period of political instability ensued during the rest of the decade, and wildlife suffered grievously (Spillet and Tamang 1966). Catastrophic floods at the same time prompted hill people to search for new land in Chitwan, but many were still deterred by the prevalent malaria. A malaria eradication program began in 1954 as part of the Rapti valley development program, and by 1960 the entire area was declared malaria free (Bolton 1975). New roads were opened, and by 1959 the whole length of the valley was settled and 70% of the forests and grasslands were converted to agriculture (Caughley 1969). The population rose from an estimated 36,000 in 1950 to 185,000 by 1971 (Laurie 1978). At an annual rate of increase of 2.6% (Mishra 1984), the population will surpass 300,000 by 1990 without accounting for migration.

Poaching was widespread during the 1950's and there was growing international concern over the rapid decline of the rhinoceros and other animal populations (Talbot 1959; Gee 1959; Spillet and Tamang 1966). Measures to establish protected areas began in the early 1960's with the declaration of several protected areas and the removal of most villages from the south bank of the Rapti River (Bolton 1975). Habitat degradation and poaching continued, however, and elephant, buffalo and swamp deer were extirpated in the area.

A full commitment to protection of the area was made in 1973 with the establishment and staffing of the Royal Chitwan National Park (Bolton 1975). Wildlife and habitat protection has succeeded during the last 15 years to the point were Chitwan is now exporting rhinoceros to other reserves in Nepal and India (Mishra and Dinerstein 1987).

One small but important concession was made for the benefit of the local villagers, who were denied use of forest resources with the establishment of the park. Villagers are charged a nominal fee and allowed to enter the Park for two weeks each year during January to cut thatch and grass building canes (Mishra 1982a, 1984). They are allowed to cut only as much grass as they can carry out of the Park on their backs.

RESEARCH STUDY AREA

Research activities were concentrated in the Sauraha area at the eastern end of the park (Fig 1, 2). This area has the most extensive complex of grassland and riverine forest in the Park, and the highest populations of rhinoceros and other large animals (Bolton 1975; Mishra 1982a). Most of the past research on animal and plants has been done in this area from the Smithsonian/Nepal Terai Ecology Project camp in Sauraha. Logistical considerations also make this the best research area in the Park: the Park elephants, which are necessary for jungle transportation are located here, and access from Kathmandu, to markets, and to communications are better here than in the rest of the Park.

The research study area extended 9 km west from the east end of Itcharny Island to the Dumaria area, and from the south bank of the Rapti River to the edge of the sal forest, about 3 km. A narrow strip of sal forest and small meadows inside the sal forest periphery were included in the study area. The research study area was about 2300 ha.

CHAPTER II. GRASSLAND COMMUNITY ORGANIZATION

INTRODUCTION

SOUTH ASIAN GRASSLAND ECOLOGY

The climax vegetation of north India is generally considered to be semi-evergreen deciduous forest (Champion 1936; Puri 1960). Grasslands are generally classed as disturbance disclimaxes, an outcome of indiscriminate fire and livestock grazing, or secondarily as edaphic climaxes (Champion 1936; Dabadghao and Shankarnarayan 1973). Although not climax communities, they can be very stable under these influences (Champion 1936).

The term, disclimax, implies some type of aberration; but, grasslands have been a component of the north Indian landscape since mid-Miocene times, about 20 million years before present (MYBP). Pollen records indicate widespread mesophyllous grasslands during the Siwalik period, which ranged from the Miocene to the Pleistocene periods (Mathur 1984; Badgely 1984; Gaur 1987). The fossil record also revealed an abundant and diverse fauna of large mammalian herbivores dominated by bovids, cervids, girrafids, suids, rhinocerotids, and proboscideans (Wadia 1953; Badam 1984; Gaur 1987). A reconstruction of the herbivore community through dental characteristics revealed a community adapted to a mosaic of low-lying mesic grassland, savanna, and broadleaf deciduous forest (Badgely 1984; West 1984), very much similar to what is found today in protected areas (Gaur 1987).

Fluvial processes were the primary forces in the formation of large-scale pattern and moisture gradients in the Siwalik plant communities (Wadia 1953; West 1984). The tectonic rise of the Himalaya and their consequent erosion by monsoonal rains lead to the formation of a vast river basin, the Siwalik basin, at the foot of the Himalayas (Wadia 1953; Mathur 1984; Vishnu-Mittre 1984; West 1984).

Layer upon layer of alluvial deposits attest to rapid changes in the Siwalik basin from 13 to 1 MYBP (West 1984). Drill holes have recovered alluvial sediment at the base of the Himalayas from a depth of 5000 m (Carson et. al. 1986).

Fluvial action remains an important disturbance effecting spatial pattern and the organization along soil gradients of contemporary Terai plant communities (Seidensticker 1976). In contrast to these sub-Himalayan grasslands, fluvial processes play a minor role in the world-wide occurrence of most grasslands, which are controlled by the lack of or over-abundance of water stemming from the interaction of climatic and edaphic factors (Tinley 1982; Sarmiento 1983; Knoop and Walker 1985; Cole 1986).

Other disturbances known to influence the organization of contemporary grasslands were also present during the Siwalik period. Fire likely was common in south Asian grasslands before the appearance of humans. Charcoal deposits indicate that fire was present in the earliest Devonian forests 400 MYBP (Collinson and Scott 1987). Fire is evident in the early fossil record of Pliocene South American savannas before the appearance of hominids (*Ramapithecus*) 9 MYBP (van der Hammen 1983). Burning by man has been considered a primary factor in the formation of south Asian plant communities (Champion 1936; Bor 1960; Dabadghao and Shankarnarayan 1973; Blasco 1983), for perhaps the last 5000 years (Wharton 1968). Gillisson (1983) attributes the presence of Australian savannas to the use of fire by aborigines for the past 32,000 years.

The abundant, large-herbivore fauna (West 1984; Badgely 1984; Gaur 1987) doubtless exerted some influence on plant communities as consumers and disturbance agents, as in contemporary grasslands (McNaughton 1979, 1983, 1985a; McNaughton et. al. 1982; Cumming 1982; Mack and Thompson 1983; Loucks et. al. 1985; Belsky 1986a, b; Collins 1987). Many of the genera that evolved during the Siwalik period are still extant (Badam 1984; Badgely 1984; West 1984). The effects of large, wild herbivores on contemporary south-Asian grasslands, however, has been considered inconsequential (Bor 1960; Dabadghao and Shankarnarayan 1973), but is largely unknown. Few studies have explored the grass-herbivore relationship.

What distinguishes sub-Himalayan grasslands as a research topic is a highly dynamic, tall grassland and woodland landscape mosaic in which a large and diverse mammalian herbivore fauna has evolved. One would expect coevolutionary grass-ungulate relationships to be weak, conforming to a model in which herbivores have little influence on vegetation (Crawley 1983). This is in contrast to the more widespread and shorter savanna grasslands of East Africa and North America, that have had or still support high herbivore biomass, and where disturbance occurs at a smaller, less dynamic scale (Collins and Barber 1985; Belsky 1986b, 1987b; McNaughton et. al. 1982; McNaughton 1983) and seems relatively less important at the landscape level. One would expect a more tightly coevolved grass-ungulate relationship (McNaughton 1979a, 1979b; Stebbins 1981; McNaughton et. al. 1982; Dyer et. al. 1982; Mack and Thompson 1984; among others) conforming to the models of Caughley (1979), Caughley and Lawton (1981), Noy-Meir (1975, 1982), and Crawley 1983). My dissertation will explore the primary production element of south Asian grass-ungulate relationships with research on plant community ecology.

ECOLOGY OF CHITWAN GRASSLANDS

Grassland or Savanna?

Most attempts at a definition of savanna have included true grasslands as a savanna type at the treeless end of the woody-component gradient (Huntley and Walker 1982; Bourliere 1983; Cole 1986). Chitwan grasslands fall within the full range of the woody savanna gradient described by Cole (1986); but, there are somewhat more treeless swards than wooded savanna. Chitwan grasslands should probably be called savanna-grasslands (Coupland 1979); but, I prefer more simply to use grasslands to describe in a general sense the Chitwan communities dominated by grasses. The terms savanna and woodland will be sparingly used to emphasize a progressive importance of trees. The vagueness or inconsistency of my distinctions are not unprecedented in the literature (see Bourliere 1983).

Equilibrium and Disturbance Processes

At the landscape level, fluvial action is the most important disturbance agent creating large-scale spatial pattern by bank cutting and channel changes (Seidensticker 1976). Former river channels are evident from the numerous terraces, old channel banks, and oxbow lakes (Fig. 2). Locally, the floodplain seems to be widening; but, there are few data to reliably indicate that sedimentation and flooding are greater now, due to recent deforestation in the hills, than in the past (Carson et. al. 1986). The historically volatile nature of Himalayan river action is evident from the westward movement of the Sapta Kosi River, by sedimentation and erosion, over 100 km to the west during the last 230 years (Carson et. al. 1986). Fluvial action also acts indirectly on plant communities by altering the soil moisture gradient with changing channels.

A soil-moisture gradient appears to be the primary environmental variable controlling among-habitat organization of Chitwan's edaphic and successional grasslands (Seidensticker 1976). Conventional thought puts sal forest at the extreme dry end of the soil-moisture gradient. Riverine forests occupy the intermediate portions of the gradient. Tall grasslands are found in the most hydric areas, and are considered an "edaphic climax" (Dabadghao and

Shankarnarayan 1973); in fact, grass associations occur within a wide range of soil moisture conditions (pers. obs.).

Deliberate burning has been a common practice among indigenous and transplanted people in the Chitwan valley (Bolton 1975). The current annual burning regime is not managed, and begins with the unauthorized firing of grasses during and after the legal cutting season in late January. More than 80% of the grassland burns at that time (pers. obs.). Anthropogenic fires from various sources continue through May, first burning most of the remaining grasslands and later much of the sal forest understory. Season, frequency, and intensity of fire covary generating manifold effects on community structure and succession (Daubenmire 1968; Vogle 1974; Bazzaz and Parrish 1982; Gillon 1983; among others), i.e., a gradient of fire effects (Loucks et. al. 1985). The fires are generally considered by Park personnel to be beneficial to the wild grazers in stimulating immediate regrowth from dormancy, and for sustained grass production.

A question arises about the equivalence of natural and anthropogenic fire. Lighting-caused fires are most likely to occur when convection storms sweep the area during April-May, several months later than the current burning season. The ensuing natural fires would likely be less frequent and more limited in extent than man-caused fires, especially if lighting storms were accompanied by rain. Grasses and woody plants initiate regrowth during April, and damage to new growth from April fires would be much greater than from fires during January and February. April is the height of the hot dry season; late fires and their effects would probably be more intense and extensive during April than during January.

The density of large mammalian herbivores in the tall grass-riverine forest mosaic of Chitwan is about 185 kg ha^{-1}, rivaling that of many East African areas (Seidensticker 1976; Eisenberg and Seidensticker 1976). Large herbivores could have a large impact on community organization as consumers, as is the case in the Serengeti were they reportedly consume up to 80% of standing biomass (McNaughton 1976, 1985a; but see Deshmukh 1986). Rhinoceros are solitary grazers that comprise nearly 85% of the Chitwan herbivore biomass (Seidensticker 1976), and have a high potential impact on the grassland system. Over 40 domestic elephants, kept by the Park and hotel concessions require substantial amounts of grass and tree fodder for their year-round subsistence. Most of the four deer species rely on the grassland plants for food during part of the year (Mishra 1982a). Past influences by extirpated herds of primary grassland species, such as wild elephant, water buffalo (*Bubalus bubalis*), and swamp deer are unknown, but were probably considerable judging by reports of animal abundance from the late 19th and early 20th centuries (Inglis 1892; Pollock and Thom 1900).

Large herbivores also influence grassland structure by physical disturbance, altering nutrient availability, and seed dispersal (McNaughton et. al. 1982; McNaughton 1983; Cumming 1982; Collins and Barber 1985; Belsky 1986b). Asian rhinoceros create small, localized grazing lawns, defecate in latrines resulting in highly fertilized islands that allow establishment of other plant species, and disperse seed and increase germination of the tree *Trewia nudiflora* (Dinerstein and Wemmer 1988). Wild boar (*Sus scrofa*) uproot tall grasses and create small cleared patches while rooting for invertebrates in tall grasses (pers. obs.).

An effect of past agriculture in the Park has been the establishment of large areas of *Imperata cylindrica*, a persistent, fire-adapted species (Hubbard et. al. 1944; Bor 1960; Eussen and Wirjahardja 1973). Domestic livestock grazing occurred in the Park until about 1974. Villagers have traditionally been allowed in the Park for 15 days during January of each year to cut *Imperata cylindrica* for thatch and the canes of tall grasses for building materials (Mishra 1982b). About 11,000 m. tons of grass products with a value of NR 10 million ($450,000), are removed annually by nearly 60,000 people (Lehmkuhl et. al. 1988).

Succession

Primary succession is initiated on river floodplains after annual flooding or channel changes. *Saccharum spontaneum* rapidly colonizes alluvial material from transported seeds and stolon nodes (Bor 1960). Full sward development occurs after about three years (Kakde 1985). Other species, particularly *Saccharum bengalense*, become established in *Saccharum spontaneum* swards after a few years, possibly in response to facilitation of soil conditions (e.g., organic matter, moisture, surface temperature) by *Saccharum spontaneum* (pers. obs). Unless further fluvial disturbance occurs and waterlogging is not a problem, succession is inferred to progress to various mixed tall grass stages, to a savanna with *Bombax ceiba*, then to deciduous riverine forest. The climax is presumably sal (*Shorea robusta*) forest after perhaps 100-200 years (Carson et. al. 1986).

The short-term and successional responses of tall-grass stands to disturbance are poorly known. Dabadghao and Shankarnarayan (1973) described general responses for a hydric disclimax *Phragmites-Saccharum-Imperata* community-type. *Phragmites karka* dominates in an undisturbed state. Persistent cutting and burning expose the typically wet soil to desiccation, with the result that *Saccharum spontaneum* and *Imperata cylindrica* eventually dominate. Introduction of domestic grazing in addition to burning leads to dominance of *Vetiveria zizanioides*. Continued burning and grazing of *Saccharum* and *Imperata* leads to stands dominated by *Imperata*, which become depauperate if these conditions persist. Annuals such as *Sporobolus, Paspalum,* and *Chrysopogon* then gradually dominate. Swards regenerate back along the same pathways in the absence of disturbance. Grazing by wild herbivores is considered inconsequential (also see Bor 1960). Dinerstein (1979) suggested a similar scheme for succession in the Bardia Reserve of Nepal.

Dabadghao and Shankarnarayan's (1973) scenario was generalized for all of north India from a small dataset (Yadava and Singh 1977), and is not entirely satisfactory for Chitwan grasslands. It assumes only an edaphic climax dominated by *Phragmites karka* and ignores woody succession and fire effects on succession. The situation is more complex. *Phragmites* forms apparently stable associations on marshy sites, which are a small portion of the landscape (pers. obs.). Tall-grass associations occupy sites with a variety of soil moisture conditions; some as edaphic climaxes on poorly drained soils, but the largest area is occupied by tall grass associations apparently succeeding to riverine forest, and possibly sal forest. Also, *Vetiveria zyzanioides* is not very common. *Saccharum spontaneum, Imperata cylindrica,* and the grazing-tolerant annuals are widespread in Chitwan, however, and the effects of burning, cutting grass for fodder, and livestock grazing appear realistic. However, few data are available to elaborate on this scheme.

Imperata stands persist under a regular burning regime because of the plant's extensive rhizome system, habit of flowering during the fire season (Hubbard et. al. 1944; Bor 1960; Eussen and Wirjahardja 1973), and the putative allelopathic properties of litter and roots (Eussen and Wirjahardja 1973; Eussen and Niemann 1981). Nevertheless, *Imperata* is very sensitive to shading (Hubbard et. al. 1944; Eussen and Wirjahardja 1973), and stands are subject to invasion and replacement by fire-resistant tall grasses, perennial forbs, and woody species, notably by the forb *Eupatorium* (*E. odoratum* and *E. adenophorum*; Compositae) (Falvey and Hengmichai 1979; Saxena and Ramakrishnan 1983). Deep root systems, relatively tall canopy, and fast growth after fire are characteristics of invading species (Eussen and Wirjahardja 1973).

Imperata stands are valuable for landscape diversity, as foraging patches, and as thatch for local development. The processes of succession to tall grass are poorly known and merit research.

OBJECTIVES AND HYPOTHESES

The objectives of the landscape and community studies are: 1) describe and model changes in the distribution of grassland and riverine forest patches over time to examine landscape stability and management; 2) classify grassland types to express their floristic and successional relationships; 3) examine community floristic data for environmental and disturbance gradients underlying grassland organization at the among-habitat (beta) level; 4) investigate within-habitat (alpha) level population processes underlying succession.

The research is primarily exploratory (Poore 1955; Gauch 1982). However, the foregoing discussion has generated several ecological and management hypotheses that the research intends to test through field research and simulation modeling.

Landscape Dynamics

Hypothesis: The regressive force of fluvial action is balanced by progressive successional processes in maintaining a stable distribution of grassland and riverine forest types in a "shifting mosaic" (*sensu* Bormann and Likens 1979; Heinselman 1981).

Landscape Management

Hypothesis: Fire suppression will slow successional change to riverine forest, which will decline in area, and floodplain types will dominate the landscape. Fire increases the rate of succession to riverine forest by eliminating dense herbaceous ground cover, which prevents the establishment of tree seedlings.

Hypothesis: Fire suppression will speed successional change to riverine forest, which will increase in area and be a dominant landscape habitat type. Fire decreases the rate of succession to riverine forest by killing woody plant regeneration.

Hypothesis: River stabilization for the protection of agricultural lands adjacent to the Park would significantly alter natural landscape patterns by decreasing fluvial disturbance and changing patterns of landscape succession.

Organization Along Gradients

Hypothesis: Grass species distributions are predominantly influenced by a soil-moisture gradient.

Hypothesis: Annual fires are pervasive, but, temporal and spatial variability of occurrence and intensity lead to a disturbance gradient in retarding succession to riverine deciduous forest.

Successional Processes

Hypothesis: *Saccharum spontaneum* dominance of early succession on recent floodplain is primarily a function of rapid colonization of sandbars primarily from flood-dispersed propagules. The later successional species *Imperata* *cylindrica*, *Saccharum bengalense*, and *Narenga porphorycoma* primarily disperse by seed during the dry season, when they cannot become established on sandbars.

Hypothesis: Succession from *Saccharum spontaneum* to a mixed tall-grass type, initially dominated by *Saccharum bengalense*, follows the facilitation model (McCormick 1968; Connell and Slatyer 1977).

Hypothesis: Secondary succession on abandoned farmland from *Imperata cylindrica* to tall grasses follows the inhibition model (McCormick 1968; Connell and Slatyer 1977), due to a combination in *I. cylindrica* of high fire resistance, sod-forming life history with high competitive ability, and putative allelopathic properties.

METHODS

LANDSCAPE DYNAMICS

Black & white aerial photographs from 1964 and 1981 were used to examine landscape dynamics. I also attempted to procure photographs taken in 1954, but was unable to locate them. Photographs from 1964 were at 1:12,000 scale; 1981 photographs were at 1:35,000 scale.

Thirteen habitat types were recognized on the aerial photographs. Floodplain and other areas outside the Park were included if they could later become part of the Park through erosion (the Park boundary is the middle of the river channel), or to examine the expansion of floodplain at the expense of agriculture.

The rate of successional change from habitat types (x_i) was determined by the linear equation (Shugart et. al. 1973),

$$dx_i/dt = f_i + \Sigma a_{ij} x_j;\quad i = 1,\ldots,n,$$

where, f_i = input to the ith state from outside the Park

a_{ij} = transfer rate to the ith from the jth state

x_j = area in the jth successional/habitat state

n = the number of states

Input from land outside the Park was determined as a constant input, f_i, from a base of 1000 ha. The matrix of simultaneous differential equations were solved by the fourth-order Runge-Kutta numerical approximation technique with a timestep of one year. Model code was adapted from Swartzman and Kaluzny (1987).

Transfer rate parameters were estimated by comparing cover type changes from 1964 to 1981 at 3472 point locations on 1:12,000-scale map overlays, drawn from 1964 and 1981 aerial photographs. Each point was characterized by cover type in 1964 and 1981 to determine type changes from succession or erosion. A transfer matrix was developed that indicated transfers to and from each cover state.

The 17-year period between the two photo years presented a small problem in determining transitions between types, and estimating the rate of transfer out of a compartment. For example, a point in the river channel in 1964 may have been tallied as savanna for 1981. The point changed from the river channel to savanna, but the intermediate transitions were unknown. In those cases, points from 1981 were pooled into the habitat type immediately succeeding the 1964 type, in a theoretical successional sequence, to estimate the rate of areal transfer out of the 1964 habitat type. If 1981 points were in earlier successional stages than during 1964, they were assumed to have eroded into the river and were pooled to the river channel.

Transfer rates, a_{ij} were estimated as the proportionality constant of the exponential equation (Shugart et. al. 1973). I calculated the parameter as the slope of the logged exponential function of points remaining in a habitat type by 1981 and initial number of points in the compartment during 1964, over time. Rates of change from one habitat type to several successional types were a proportion of the total transfer rate equal to the amount of area in the receiving state (Shugart et. al. 1973).

The need for calibrating the rate parameters was determined by running the model with the cover type areas during 1964 as initial conditions, and comparing calculated type areas with mapped estimates for 1981 (Swartzman and Kaluzny 1987). Rates describing transition to and from floodplain types required the most adjustment. This was not surprising because the time between photo samples was long enough to allow substantial change, and because fluvial processes are less likely to be linear than dry-land succession. Upland successional rates required minor adjustment. Rates were adjusted iteratively until model estimates of 1981 areas conformed to mapped estimates.

CLASSIFICATION AND GRADIENT ANALYSIS

Study Area and Sampling Procedure

Sample points for systematic sampling were determined from a 250 m (ground measurement) grid on an aerial photograph of the research study area. Approximately two-thirds of the area, extending 6 km west from Sauraha, was sampled with 188 plots. One hundred and sixty-eight plots were taken south of the Rapti River, and twenty plots were measured on the north side of the river, to the south of Itcharny Island. Two-thirds of the plots were spaced equally on the 250 m grid; the other third of the plots on the west side of the study area was measured on every other north-south transect of the grid for a 250 x 500 m spacing.

Plot locations were located with the aid of aerial photographs and compass. Transect distances were measured from elephant-back by consecutive measurement with a 50 m rope.

Minimum plot sizes (Mueller-Dombois and Ellenberg 1974) were determined by preliminary sampling in *Saccharum spontaneum* and *Narenga porphorycoma* grassland types and in riverine forest. A plot area on the species-area curves was selected that included at least 90% of the total number of observed species (Fig. 5). The riverine forest plot area was used for sampling sal forest; sal forest understory is less diverse than riverine forest but more diverse than grassland so I felt the riverine forest plot size would be adequate.

Minimum-area plots of 8.5 x 8.5 m were marked for grassland sample points, but 11 x 11 m plots were used in riverine forest. All understory species within the plot were listed and cover/abundance was rated on the Domin scale (1-10, or a "+" for solitary plants) (Mueller-Dombois and Ellenberg 1974). Unknown species were described, numbered, and collected for later identification. Notes were made of tree species inside and outside the plot, and of understory species occurring outside but not inside the plot.

Data Analysis

Domin cover-abundance values of "+" (solitary, cover insignificant) were grouped with the "1" values (scarce, cover insignificant) to conform to a 1-10 scale for computational simplicity. I think there was very little information lost by grouping these two classes, because the difference between the two ratings is relatively minor.

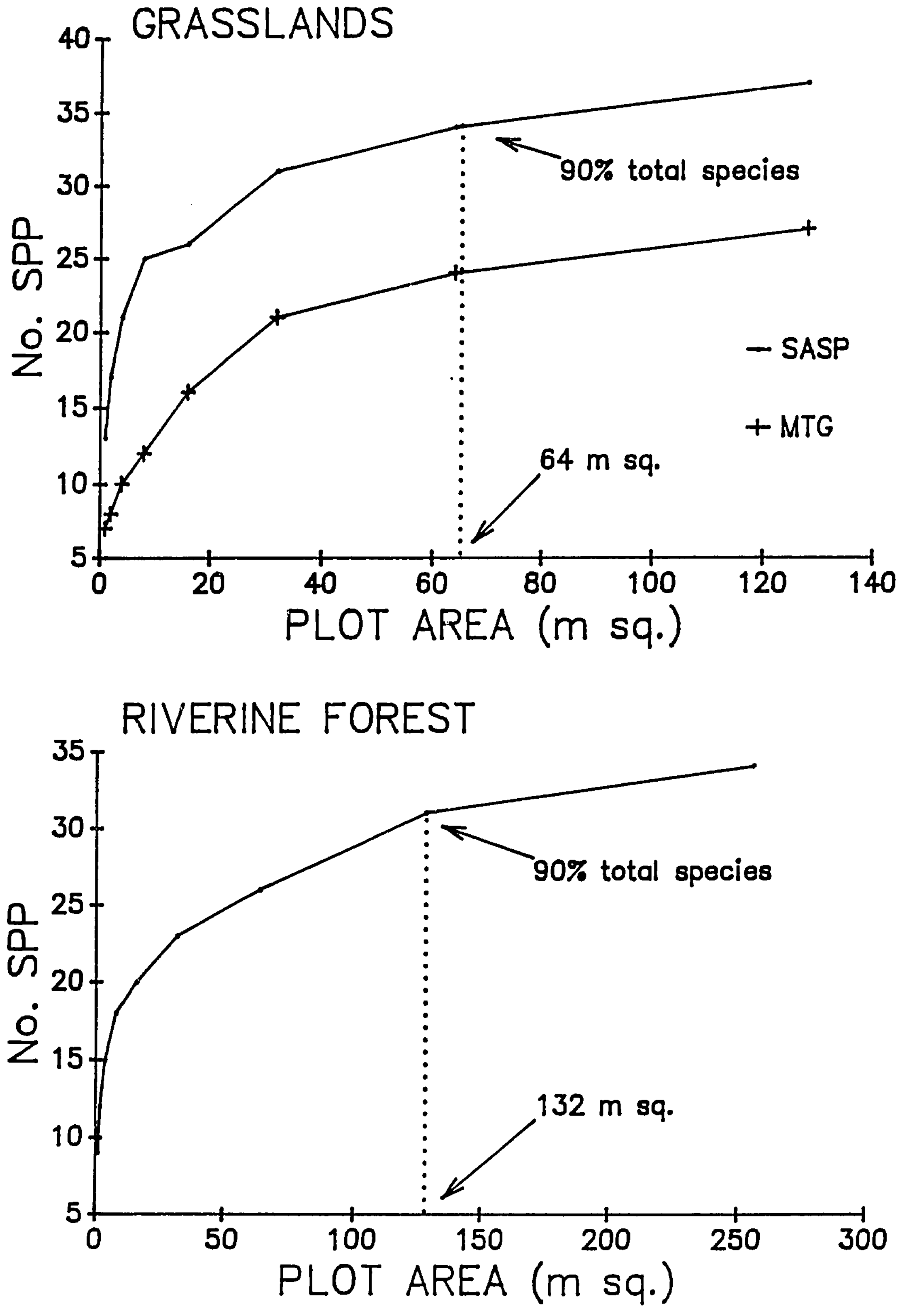

Fig. 5. Species-area curves for (*A*) *Saccharum spontaneum* and Mixed Tall Grass grassland types, and (*B*) deciduous riverine forest understory.

Sample and species classifications were performed by polythetic divisive clustering with the TWINSPAN program (Hill 1979a). The classification was limited to a maximum of five division levels, because cluster size became too small for reliable interpretation with more divisions. Psuedospecies cut levels were set to group psuedospecies in five categories of less than 1% cover, 1-10% cover, 11-33% cover, 34-75% cover, and >75% cover. All other program options were at default levels.

Gradient analysis was done by detrended correspondence analysis with the DECORANA program (Hill 1979b). Downweighting of rare species was the only option employed to refine the ordinations.

SUCCESSION EXPERIMENTS

Sandbar Succession

An experiment was designed to investigate the methods of grass colonization on new river sandbars. A 100 m^2 area of new sandbar was enclosed with barbed wire, and 49, 1 m^2 plots were laid out with 0.5 m buffers. Seven propagation treatments were arranged in a randomized block design with seven replicates. Treatments were: 1) *Saccharum spontaneum* seeds; 2) *Saccharum spontaneum* stolon nodes buried 5 cm; 3) *Saccharum spontaneum* stolon nodes on the surface; 4) *Imperata cylindrica* seeds; 5) *Saccharum bengalense* seeds; 6) *Narenga porphorycoma* seeds; and 7) a control with no seeds or nodes planted. Seeds were covered with a thin layer of sand to keep them from blowing away.

Saccharum spontaneum seeds were planted on 15 November 1985, the very end of the seed dispersal period. Five grams of seeds were scattered over the plots and watered. Twenty-five *Saccharum spontaneum* nodes, 6 cm long, were placed on the surface for one treatment, and planted at 3 cm depth for another treatment. Seeds and nodes were watered for ten days to simulate post-monsoon rains during mid-October, because planting was somewhat later than peak seed dispersal during post-monsoon showers. I considered watering justified to simulate conditions present earlier in the month. I did not plant earlier in fear of late floods destroying the site.

Saccharum bengalense and *Narenga porphorycoma* seeds were planted on 14 December, during the period of seed dispersal. *Imperata cylindrica* seeds were planted during late May. Plots with these three species were not watered.

Plots were inspected periodically until just before the expected monsoon floods, during the first week of July 1986, when the experiment was terminated.

Imperata cylindrica to Tall Grass Succession

I designed two experiments to examine the question of which successional model, facilitation, tolerance, or inhibition (McCormick 1968; Connell and Slatyer 1977) conformed to species replacement processes in grassland.

Six treatments with five replicates were made in an *Imperata cylindrica* sward to examine succession to *Saccharum spontaneum* and *Narenga porphorycoma* tall-grass species. Plots 1 m^2 were arranged in a randomized block design. Twenty-five tillers of a tall grass species were planted with and without *Imperata cylindrica* for treatments: 1) *Narenga porphorycoma* with *Imperata cylindrica*; 2) *Narenga porphorycoma* without *Imperata cylindrica*; 3) *Saccharum spontaneum* with *Imperata cylindrica*; 4) *Saccharum spontaneum* without *Imperata cylindrica*; 5) no *Imperata cylindrica* and no tall-grass species; and 6) *Imperata cylindrica* and no tall-grass species.

Plots without *Imperata cylindrica* were scraped at the ground surface to remove *Imperata*, and weeded as necessary. Twenty-five tillers of the tall-grass species, each about 30 cm long with a root node and primary roots, were planted with equal spacing. I started the experiment on 20 March 1986, but the site was too far away to water regularly, and the tillers died from the heat. Tillers were successfully replanted on 13 July 1986. At the end of the experiment on 15 January 1987, the planted tillers were clipped at ground level, and number of live stems and total live dry weight were recorded. Treatment effects were determined by analysis of variance.

A similar experiment was setup at a *Saccharum spontaneum* site with *Saccharum bengalense* as the only successional species. I started the experiment on 17 July 1986, but two successive floods destroyed the site within a few months and there was not sufficient time to repeat the experiment.

RESULTS

LANDSCAPE DYNAMICS

Habitat Areal Changes

The most remarkable landscape changes occurred in the general floodplain (Table 1). River channel area increased by 56%. Floodplain (sandbars and perennial inundated areas) inside the park increased by 215%, and outside the Park by 121% from 1964. The increase in Park floodplain habitats was greater because the river channel is bank-cutting mostly non-Park lands and depositing on the Park-side of the channel.

Table 1. Area (hectares) and percentages of general habitat types in research study area, Royal Chitwan National Park, Nepal, in 1964 and 1981.

	1964		1981		Ha	%
	Area	%	Area	%	+/-	+/-
Non-Park Land						
Outside-Park Lands	97	3.2	0	0.0	-97	na
Non-Park Floodplain	50	1.6	110	3.6	60	121.1
Non-Park *Saccharum spontaneum*	76	2.5	91	3.0	16	20.7
Park Land						
River Channel	157	5.2	245	8.1	88	56.1
Floodplain	52	1.7	165	5.4	112	215.0
Saccharum spontaneum	362	12.0	435	14.4	73	20.2
Mixed Tall Grass	546	18.1	393	13.0	-153	-28.1
MTG-*Imperata cylindrica* Mosaic	0	0.0	51	1.7	51	na
Themeda-Imperata Mixture	133	4.4	459	15.2	326	244.4
Bombax-Tall Grass Savanna	207	6.9	509	16.8	301	145.4
Riverine Forest	405	13.4	473	15.6	68	16.8
Sal Woodland	6	0.2	6	0.2	0	0.0
Sal Forest	88	2.9	88	2.9	0	0.0
Reclaimed Agriculture						
Agriculture (treeless)	537	17.7	0	0.0	-537	-100.0
Agriculture (woodland)	309	10.2	0	0.0	-309	-100.0
Total hectares	3025		3025			

Secondary floodplain vegetated with *Saccharum spontaneum* increased by 20% both inside and outside the Park. A large part of the increase was concentrated in the vicinity of Sauraha where the Rapti River makes a wide S-shaped curve. Much of this change was inside the Park; a large part of Itcharny Island riverine forest was changed into *Saccharum spontaneum* and floodplain. A smaller area of outside-Park agricultural land was lost to erosion. The greatest loss of agricultural land occurred in the vicinity of Sauraha and downstream at Badrani. Quite a large area (133 ha) of mixed tall grassland, and some savanna and riverine forest was lost from the Park down river from Sauraha, below the mouth of Dudhwara Khola (creek).

Park area increased only slightly during the 17-year interval between photographs. Table 1 does not show an increase in area, however, because the sampling procedure required a constant area to determine successional transfers. Simple calculations show that all non-Park lands had a net decrease of 22 ha. However, considering only net change hides the loss of about 45 ha of high-quality agricultural land (part of the "outside-park Lands", Table 1) to the floodplain; the increase of non-Park floodplain offset the loss in the net change calculation.

The largest and most predictable, changes came from the reclamation of agricultural land abandoned in 1964. About 846 ha were gained. After abandonment, most of this land initially was dominated by *Imperata cylindrica* (Bolton 1975), a persistent tropical weedy grass (Hubbard et; al. 1944; Bor 1960). Tall grasses quickly began to invade these sites, and now form pure or mosaic stands over much of the area. A MTG/*Imperata cylindrica* Mosaic (Table 1) was not identified in the 1964 photos because photos were taken while agriculture still was present.

Landscape Topology and Rates of Change

One immediately discerns from the system topology that the river channel is the focus of landscape dynamics (Fig. 6). Three subsystems are evident in the system topology. Non-Park floodplain habitats are one subsystem. They are rather artificially partitioned from the Park floodplain, but they reveal slightly different dynamics due to topographic variation and river channel characteristics.

Rates of change from river channel to primary floodplain, and from floodplain to *Saccharum* are nearly equal, regardless of ownership. However, non-Park *Saccharum* returns to the river channel four times faster than Park *Saccharum*, indicating little successional progression of non-Park *Saccharum* to upland habitats. This phenomenon is due to active bank cutting of non-Park lands and sediment deposition on the opposite, Park side, of the channel. The rate of transfer to "other outside lands" is missing because these areas were outside the immediate study area and not of principle interest.

The main subsystem consists of Park floodplain and upland habitats. Transfer rates indicate increasing *Saccharum* habitat because the loss rate to mixed tall grass (MTG) succession and erosion to the river channel is one-fourth the rate of input from the floodplain (Fig. 6). The rate of succession increases with the MTG to savanna transition, which is double the *Saccharum* to MTG rate. Change from savanna to riverine forest is slightly slower than the MTG to savanna rate. Erosion rates of *Saccharum*, MTG, savanna, and riverine forest to river channel are on the order of half the input rate for all the habitats past the *Saccharum* stage.

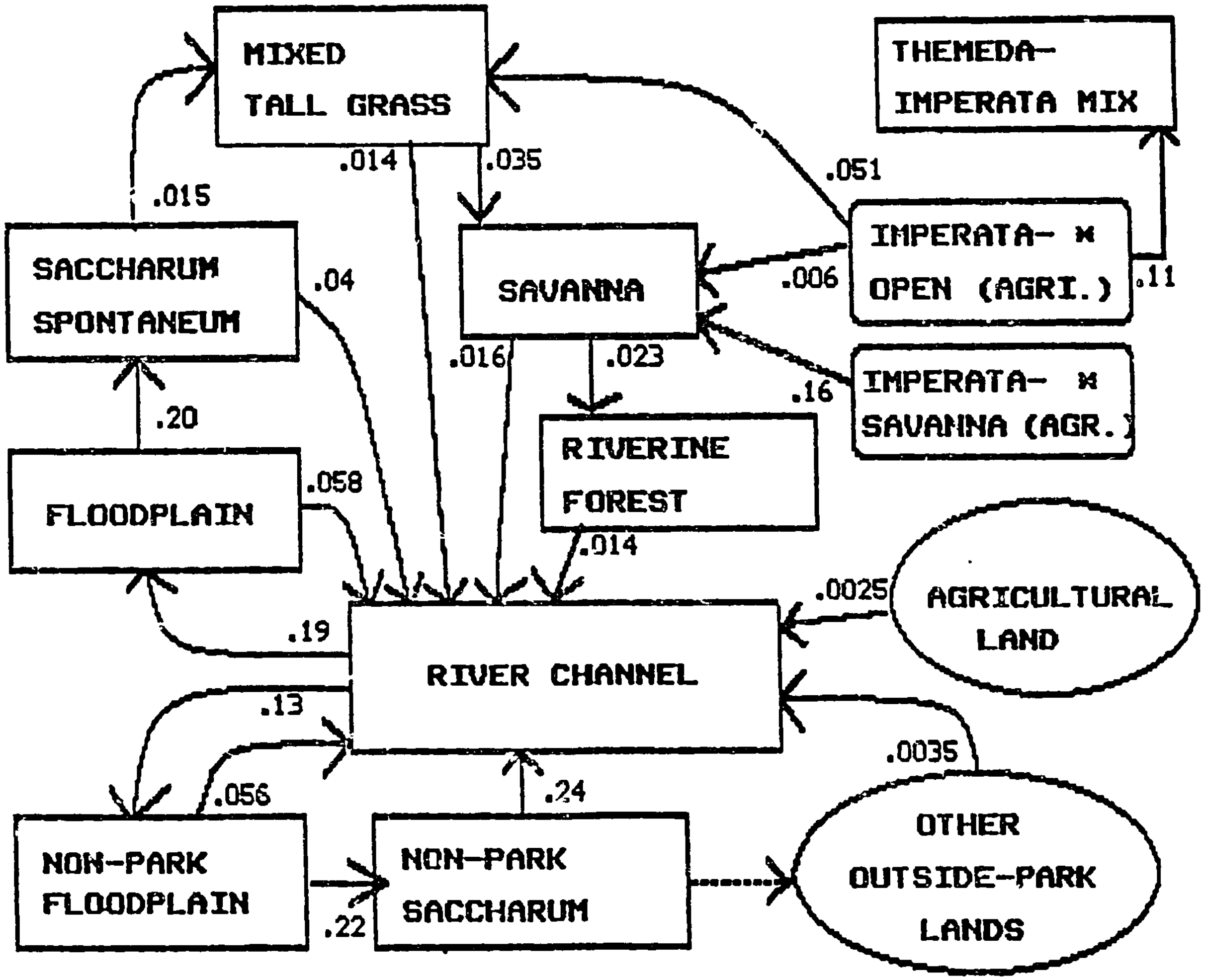

Fig. 6. A model of landscape dynamics for natural upland and floodplain communities in Royal Chitwan National Park. Numbers are instantaneous rates of area transfer.

The third landscape circulation system is the one-way succession of reclaimed farm land into the main subsystem (Fig. 6). *Imperata cylindrica* quickly colonized this area (Bolton 1975) from weedy survivors of agriculture, from the seed bank, or from fresh seed dispersal. Succession from paddy fields (*Imperata*-Open Agr.), with a high water table, was primarily to a *Themeda-Imperata* Mixture, but some area succeeded to mixed tall grass at about half that rate. Dryer areas (*Imperata*-savanna Agr.) succeeded primarily to MTG savanna. The former savanna nature of these sites was evident from the 1964 aerial photographs, which showed large trees remaining in the farm fields.

Model Simulations

Current conditions.--a 50-year simulation starting with habitat areas during 1981, the last year for which habitat type areas were measured from aerial photographs, suggests that the landscape is not at equilibrium, or a shifting mosaic (Fig. 7A). The *Saccharum spontaneum* type , the first successional stage leading to riverine forest on the floodplain, nearly doubles in area; whereas, the intermediate stages, mixed tall grass and woodland, decline by 50 %. Agricultural lands, other non-park lands, and non-floodplain types erode into the river channel, but fairly rapidly move into the *Saccharum spontaneum* type, from which succession to later stages is much slower than the rate of fluvial disturbance. This trend indicates a clear dominance of fluvial disturbance over successional processes in forming landscape pattern.

A 200-year simulation from 1964 conditions reveals that the area of the *Saccharum spontaneum* type continues to increase, but the rate decreases slowly with time (Fig. 7B). The relative distribution of other types stabilizes after 70 years in 2050. mixed tall grass and woodland types initially decline in area,

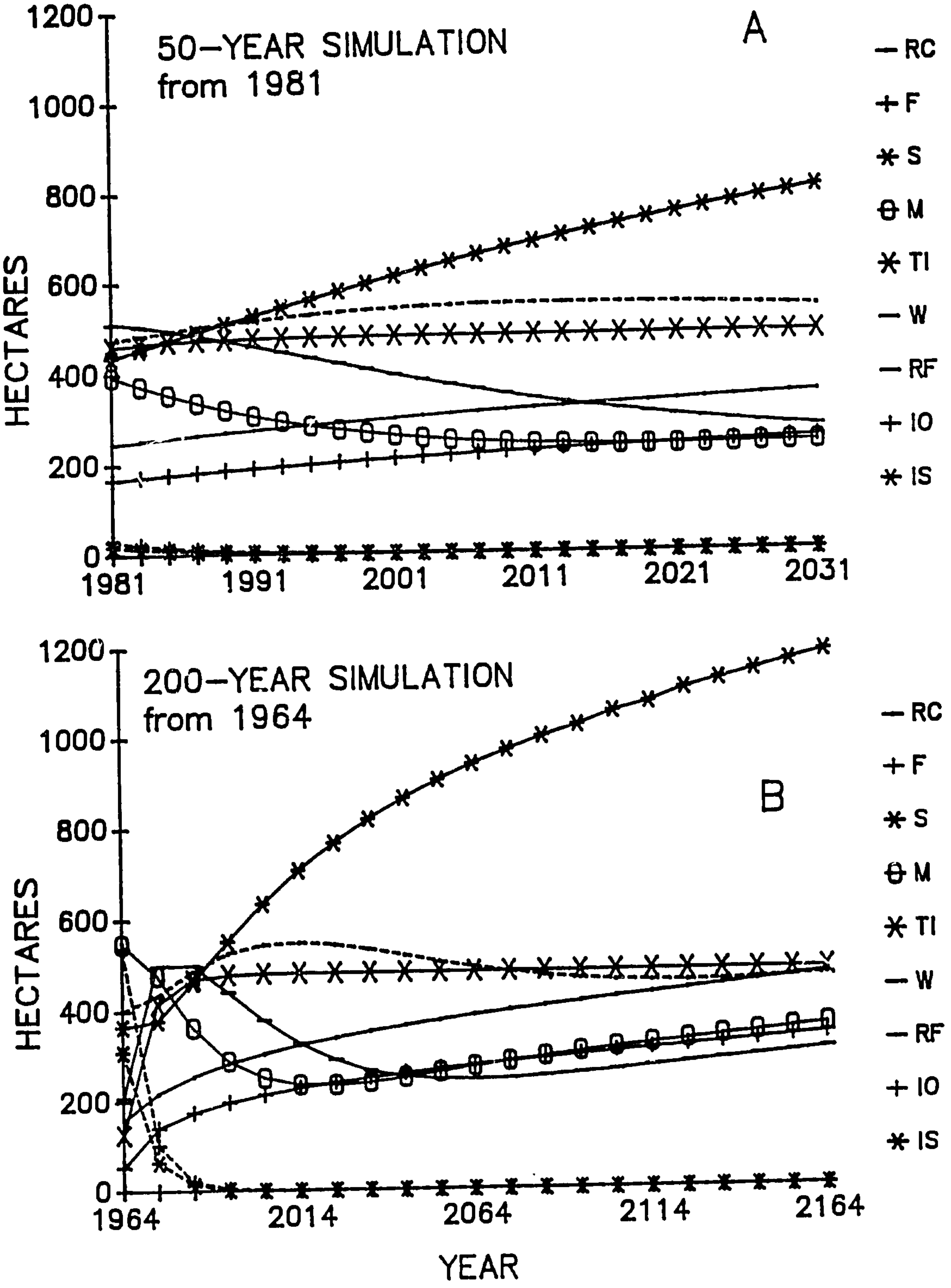

Fig. 7. Linear model simulations of landscape dynamics in study area. *A*) 50-year simulation from 1981; *B*) 200-year simulation from 1964. RC=river channel; F=floodplain; S=*Saccharum spontaneum* type; M=mixed tall grass type; TI=*Themeda/Imperata* type; W=woodland savanna; RF=riverine forest; IO=former agriculture/open; IS=former agriculture/savanna.

then begin to increase slowly. Their increase is balanced by the slight decline in the rate of *Saccharum spontaneum* increase. Areas of river channel and floodplain increase slowly, mainly from erosion of non-park lands. Succession from *the Saccharum spontaneum* type to the mixed tall grass type appears too slow to accommodate rapid floodplain inputs.

Fire suppression.--conventional thinking has given fire the role of eliminating woody regeneration and retarding succession (Daubenmire 1968; Vogle 1974; Cole 1986). To simulate the effects of fire suppression, the transfer rates from mixed tall grass to woodland, and from woodland to riverine forest were doubled. I have no *a priori* reason for doubling the transfer rate; there are no data to suggest that succession time would be halved for these types. Rather, I think that doubling the rate is a convenient limit to observe the general system response.

A 200-year simulation indicates only a short-term dominance of the landscape by riverine forest (Fig. 8A). Riverine forest increases rapidly in area for 30 years, then the rate declines slowly for about 80 years before again increasing slightly. Concurrently, areas for the mixed tall grass and woodland types decline during the first 30 years then level: a pattern unchanged from simulation with original transfer rates except that area stabilizes at lower values. The area of *Saccharum spontaneum* increases steadily, as in the initial simulations, and surpasses riverine forest as the dominant landscape element after 25 years.

A second hypothesis about the effects of fire suppression was formulated while conducting fire and production studies. Unburned tall-grass swards developed a dense mat of above-ground dead biomass, which heavily shaded the ground. Few tree seedlings or woody plants were seen to grow under those condi-

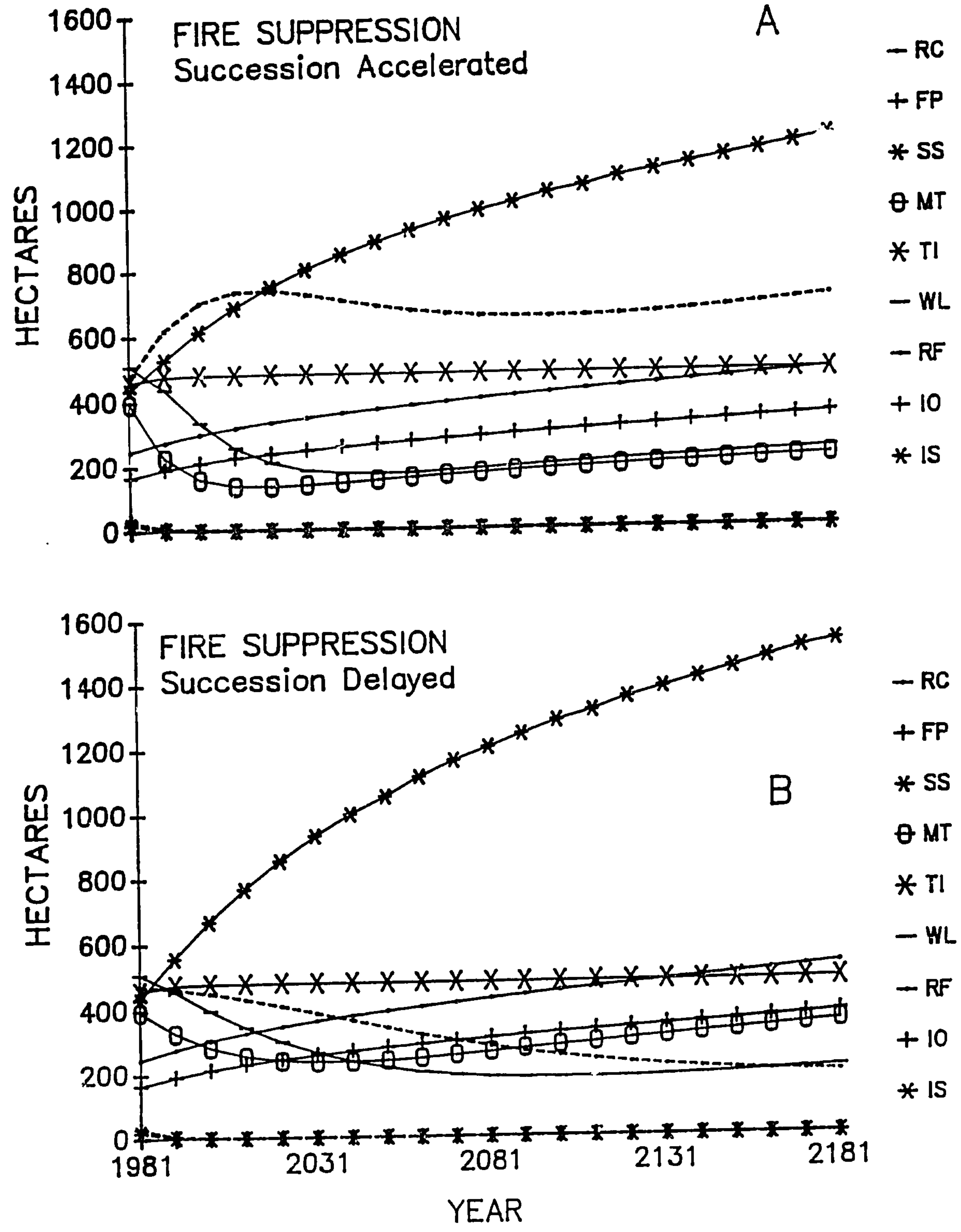

Fig. 8. Model simulations testing hypotheses on the role of fire in landscape dynamics. *A*) Fires are suppressed: succession to woody species accelerated; *B*) Fires suppressed: succession to woody species delayed.

tions. It seemed possible that fire could actually facilitate woody succession, an effect opposite than usually observed, by removing heavy litter accumulations.

Transfer rates between mixed tall grass and woodland, and from woodland to riverine forest were halved, which doubles the transition time, to test the hypothesis. A 200-year simulation shows a more rapid dominance of the landscape by *Saccharum spontaneum* than in previous simulations, and a general decline in area of all other cover types (Fig 8B). Mixed tall grass and woodland areas decline, but are slightly higher than with the previous hypothesis. Riverine forest area declines rapidly, instead of increasing as in other simulations. River channel and floodplain areas increase slightly more rapidly than with the previous hypothesis, as more material moves into the river channel through erosion of *Saccharum spontaneum*, than moves through succession to other types.

River bank stabilization.--there has been much talk among Chitwan villagers that are losing land to river erosion of stabilizing the river banks. I was interested in exploring the consequences of bank stabilization on landscape pattern. River bank stabilization was simulated by eliminating input from outside land sources of agricultural and other Lands. After 50 years, the overall pattern of change (Fig. 9) is not much different than under current conditions (Fig. 7A). About 300 ha remain outside the Park in agriculture and forest, which would otherwise be transferred to floodplain communities.

CLASSIFICATION

A total of 488 species in 188 plots were identified in the sample plots. However, species with a frequency of five or less were eliminated from the analysis, consistent with Gauch's (1982) recommendations, to yield 146 species for inclusion in the cluster analysis.

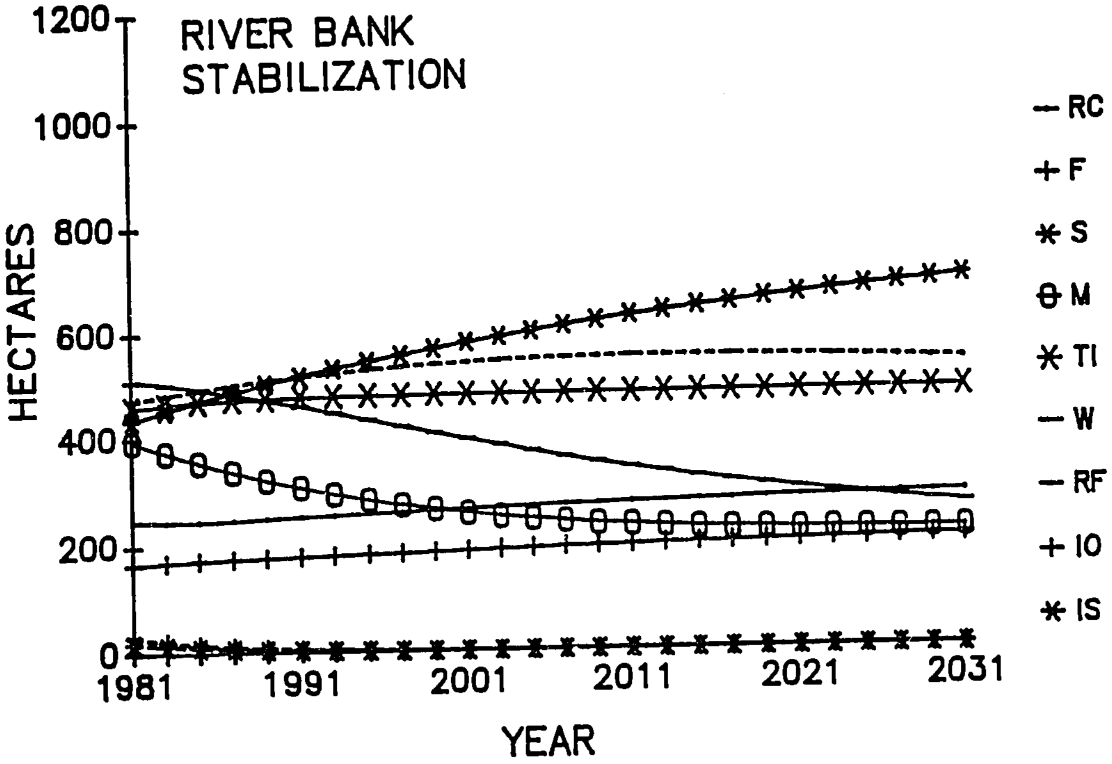

Fig. 9. Model simulation testing hypothesis that river bank stabilization will reduce landscape heterogeneity.

Ten grassland associations, with six phases, and three forest associations were identified through cluster analysis of sample plots with TWINSPAN (Fig. 10). A maximum of 32 types was possible with five levels of division in the cluster analysis. However, the final number of types was smaller because some clusters were not divided beyond the fourth level, and some fifth-level associations were pooled because they appeared to be more an artifact of small group size and variation in species occurrence among plots than natural groups.

The first division separated plots on the basis of high shrub richness, and shrub cover up to 33%. This division segregated plots on an apparent successional or shrub gradient into a "grass-shrub" cluster with riverine forests and grass-shrub ecotones dominated by *Saccharum bengalense*, and a "grassland" cluster with a very minor shrub component that included sal forest and nearly pure grass swards. Indicator species for the grass-shrub group were the riverine forest shrubs *Clerodendron viscosum, Pogostemon benghalensis,* and *Colbrookia oppositafolia,* the grass *Saccharum bengalense,* and the liana *Acacia rugosa.* The grassland types were indicated primarily by the absence of the above shrubs. Grassland types appeared to be both stable edaphic associations and successional associations. Most sal forest samples were grouped with the grassland types, but two sal stands with understory species similar to riverine forest were grouped near riverine forest in the grass-shrub cluster.

Seventy-eight percent of the samples were clustered as grassland at the first division. These stands were divided further into three groups: 1) plots dominated by *Themeda arundinacea* with a strong *Narenga porphorycoma* component (including sal forest) on mollic soils usually with a high water table; and mixed tall grass (MTG) types without *Themeda arundinacea* that were dominated by 2) *Narenga porphorycoma* on old alluvial soils, or 3) *Saccharum spontaneum* on recent floodplain alluvium. *Themeda* and *Narenga* types were sometimes in an open savanna formation with large *Bombax ceiba* trees.

The "grass-shrub" cluster, identified at the first division, contained 22% of the plots. It was separated further into riverine forest and grass-shrub associations. Grass-shrub types were dominated by *Saccharum bengalense*, with shrub cover up to 33%, and were often in open savanna with large *Bombax ceiba* or *Bauhinia malabarica*. Soils were generally well-drained Entisols. Associations with *Saccharum spontaneum* codominant tended to occur on more recent alluvium and dryer soils than types codominated by *Narenga porphorycoma*. The primary type name of *Saccharum bengalense*-Shrub is shortened below simply to "SS".

The *Saccharum bengalense*-Shrub (SS) types reveal their nature as successional stages toward riverine forest by a strong presence of riverine forest tree species as seedlings or saplings. *Premna obtusifolia*, *Bauhinia malabarica*, and *Bombax ceiba* seedlings were strongly associated with SS types. These trees are light-demanding early successional species that are common mid-story species, more aptly relict species, in riverine forests.

Association names in the following discussion use the convention of having the dominant/indicator species acronyms in sequence of clustering level, starting at the second level. Thus THAR/NAPO/IMCY indicates an association identified within the hierarchy of *Themeda arundinacea*, *Narenga porphorycoma*, and indicated by *Imperata cylindrica*. Phases have a fourth name added. Sal and riverine forests are the exception in retaining a simple descriptive name; my primary interest in sampling these types was to examine successional relationships rather than classify. Numbers in parentheses correspond to identification numbers used in Fig. 10.

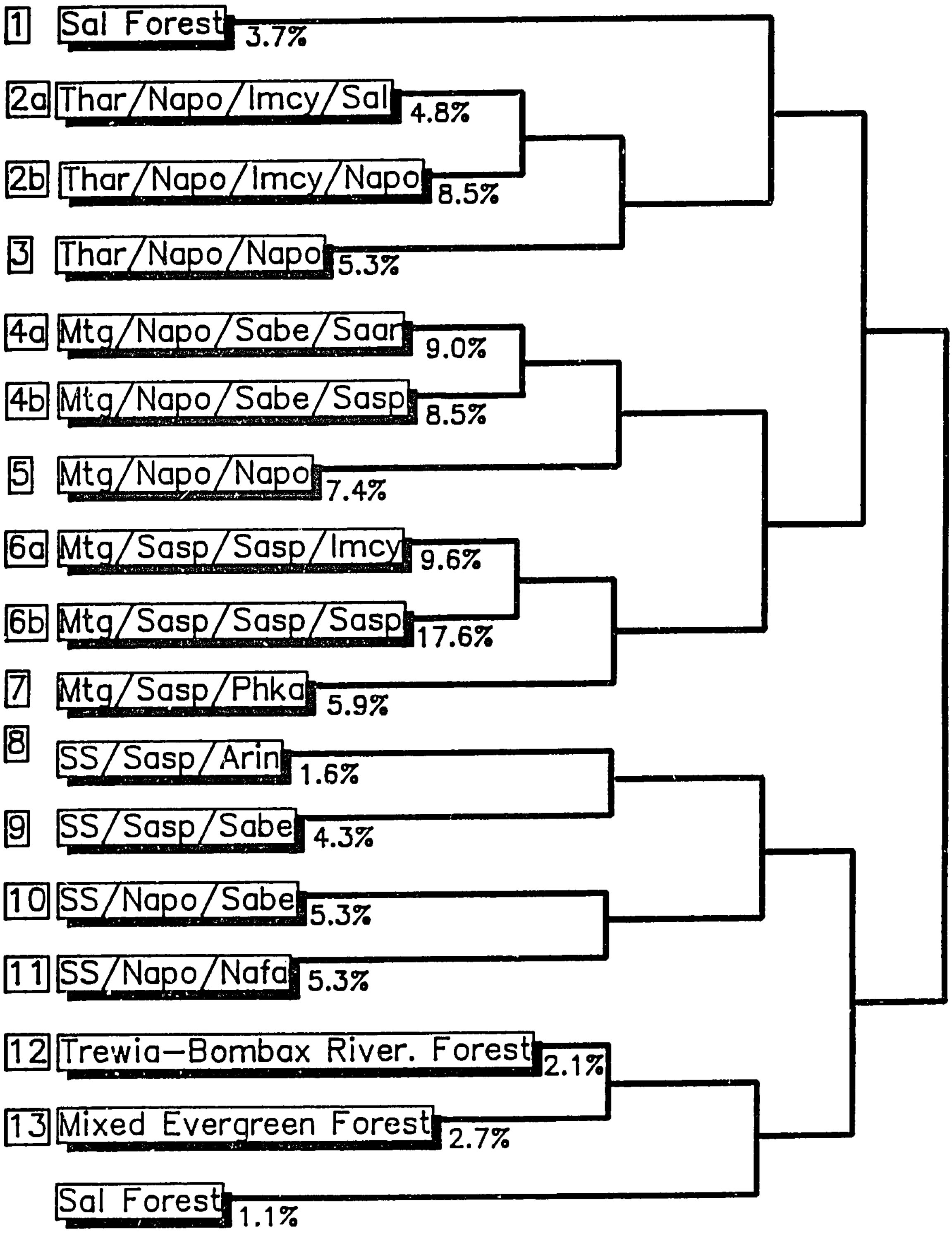

Fig. 10. Grassland and forest types identified through polythetic divisive classification (TWINSPAN) of community sampling data. Numbers at left indicate type number; at right, percentage of 188 samples in type. Sal=*Shorea robusta*; Thar=*Themeda arundinacea*; Napo=*Narenga porphorycoma*; Imcy= *Imperata cylindrica*; Mtg=Mixed Tall Grass; Sabe=*Saccharum bengalense*; Saar=*Saccharum arundinaceum*; Sasp=*Saccharum spontaneum*; Phka=*Phragmites karka*; SS=Sabe/Shrub; Arin=*Artemisia indica*; Nafa=*Narenga fallax*.

Sal Forest (1)

Sal forest stands were indicated by regeneration of the tree *Dillenia pentagyna*. Sal, *Litsea monopetala* and *Bridelia retusa* regeneration also was common. Shrub species in common with non-forest stands were *Clerodendron viscosum* and *Grewia sclerophylla*. Understory ground cover was generally very sparse, except in the two samples clustered with riverine forest. These plots had a high cover of shrubs common to riverine forest.

Themeda (Thar) Associations

Thar/Napo/Imcy (2).--codominance of *Themeda arundinacea* and *Narenga porphorycoma*, and *Imperata cylindrica* with 20-75% cover characterized this association (Fig. 11). Strongly associated grass species were *Arundinella nepalensis*, *Phragmites karka*, and *Hemarthria compressa*. Woody species had very low frequencies and cover. Soils were Mollisols on ancient terraces, most with an aquic (saturated for a significant part of the year) moisture regime, and Inceptisols. Two phases were distinguished.

Thar/Napo/Imcy/Sal (2a).--this phase was indicated by good regeneration of sal, the grasses *Arundinella nepalensis*, and the shrub *Grewia sclerophylla*. *Apluda mutica* was conspicuously absent. These samples occurred at the sal-grassland ecotone, mostly in wet meadows inside the periphery of the sal forest. Sward height varied from 1 to 4 m depending on the abundance of *Imperata cylindrica*. Soils were Mollisols with an aquic moisture regime caused by a perched water table. This phase appears to be a stable edaphic association; no changes in 1964 sward boundaries were detected from 1981 aerial photographs.

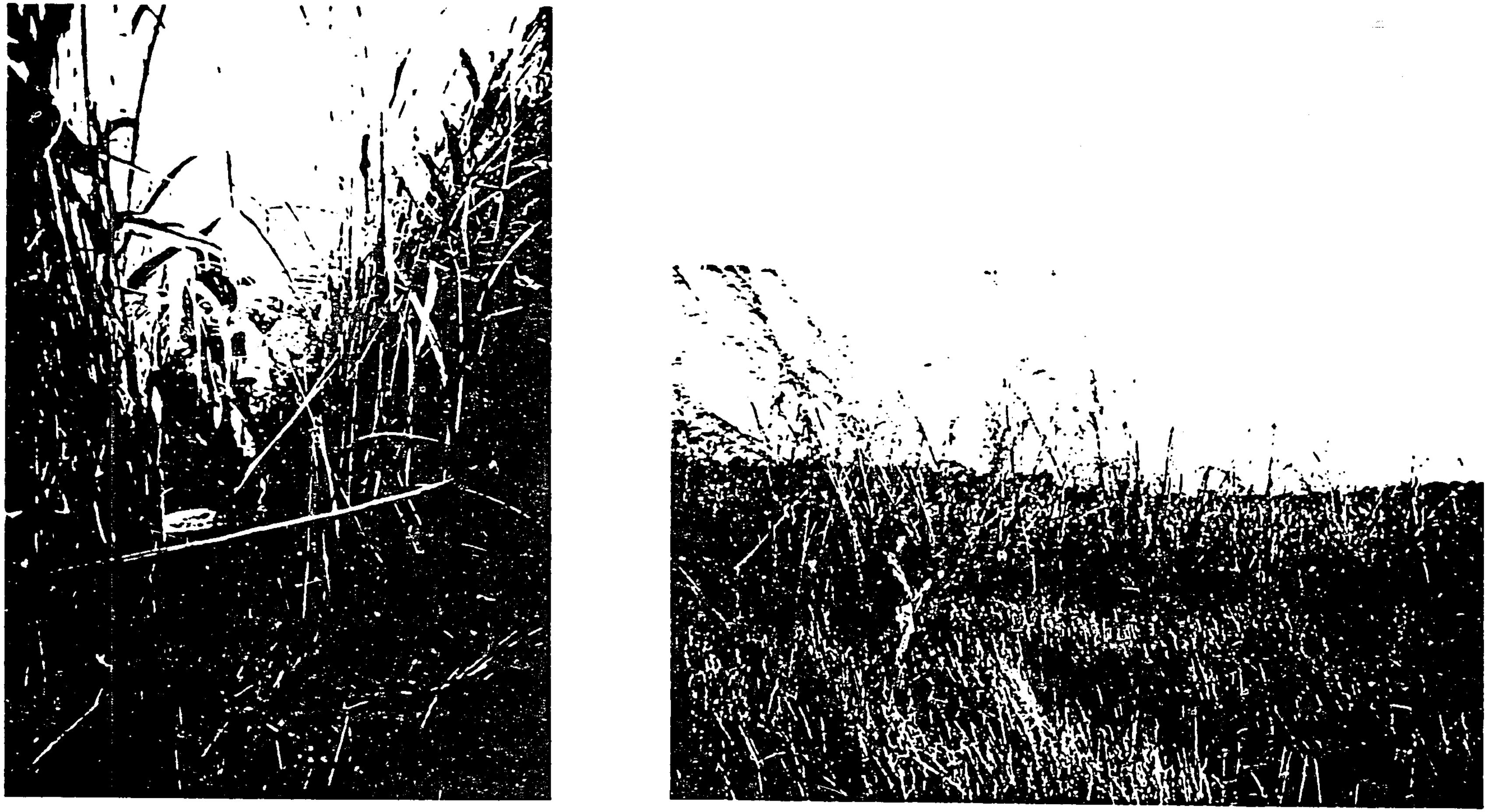

Fig. 11. Typical density of a mixed tall grass sward of *Themeda arundinacea* and *Narenga porphorycoma* (*left*); and, (*right*) *Themeda arundinacea*/ *Narenga porphorycoma*/ *Imperata cylindrica* type grassland dominated by low *Imperata cylindrica* with tall flowering culms of *Themeda arundinacea*. Site was former paddy field.

Thar/Napo/Imcy/Napo (2b).--abundant *Apluda mutica* indicated this phase. Associated grasses were *Hemarthria compressa*, *Saccharum spontaneum*, and *Phragmites karka*. These sites were former paddy fields reclaimed for Park land in 1964. The grass cover was a mixed sward, less than 1 m tall, of stunted *Themeda arundinacea* mixed with *Imperata cylindrica* in mosaic with tall dense Napo-dominated stands (Fig. 11). Soils were Mollisols with an aquic moisture regime, primarily caused by a perched water table. An impermeable pan 10-20 cm below the surface may account for the aquic moisture regime and the stunted appearance of the tall grasses. This phase appears to be a fairly stable edaphic association.

Thar/Napo/Napo (3).--*Narenga porphorycoma* dominated *Themeda arundinacea* in very dense stands. Shrub species were poorly represented, but *Piper nepalensis, Codariocalyx gyroides, Vitis auriculata*, *Desmodium gangeticum*, and *Zizyphus mauritania* were often present. This association most commonly occurred as open savanna with scattered, large *Bombax ceiba* trees. Seedlings of other trees, *Litsea monopetala*, *Premna obtusifolia*, *Trewia nudiflora*, and *Ehretia laevis*, were present in low numbers. The savanna structure and tree regeneration indicated a successional association. Soils were mostly Inceptisols with fair drainage.

Mixed Tall Grass (MTG) Associations

The absence of *Themeda arundinacea* indicated the MTG associations within the "grassland" cluster. These samples were divided into *Narenga porphorycoma* associations (Fig. 12) on old floodplain terraces, and recent floodplain *Saccharum spontaneum* associations (Fig. 13). *Narenga* MTG associations were most often associated with *Bombax ceiba* in a savanna condition. *Saccharum spontaneum*

Fig. 12. Mixed, tall *Narenga porphorycoma* grassland before burning (*top*), and after burning (*bottom*) in the vicinity of the Dumaria and the "Gaur Machan". Sal forest is in the background.

Fig. 13. Floodplain grassland habitats. Recent floodplain bordering older *Saccharum spontaneum*-vegetated floodplain (*top*); and, at the boundary of river terraces with older *Saccharum bengalense* grassland to the left and more recent floodplain with *Saccharum spontaneum* in flower on the right (*bottom*). Forest in background is riverine forest.

swards were generally tree-less grassland. Soils were generally alluvial Entisols, with poor to good drainage. These types appear to be mostly successional associations initiated on floodplains, and developing under the influence of fire, and wildlife grazing and browsing.

MTG/Napo/Sabe (4).--*Narenga porphorycoma* is codominant with *Saccharum bengalense*. *Imperata cylindrica*, *Zizyphus mauritania*, and *Grewia sclerophylla* are other indicators. Two phases were distinguished based on subdominance of *Saccharum arundinacea* or *Saccharum spontaneum*.

> MTG/Napo/Sabe/Saar (4a).--a strong presence of *Saccharum arundinacea* (Saar) indicated this phase. *Desmodium gangeticum* and *Callicarpa macrophylla* were shrub indicator species. *Narenga fallax* and *Hemarthria compressa* were strongly associated grass species. *Codariocalyx motorius*, *Securinega virosa*, and *Flemingia macrophylla* were associated shrubs. *Premna obtusifolia* and *Xeromphis uliginosa* tree regeneration were often present.
>
> MTG/Napo/Sabe/Sasp (4b).--a large component of *Saccharum spontaneum* indicated this phase, along with *Imperata cylindrica* and *Zizyphus mauritania*. Cover of *Narenga porphorycoma* was less well developed on these sites than in association 4a with *Saccharum arundinacea* and *Narenga fallax*.

MTG/Napo/Napo (5).--near complete dominance *by Narenga porphorycoma* and absence of *Saccharum bengalense* was indicated for wet sites on fairly well developed soils. *Saccharum spontaneum* was sometimes a weak associate along with *Arundo donax*, and the fern *Dryopteris* sp..

MTG/Sasp/Sasp (6).--floodplain *Saccharum spontaneum* associations were indicated by the near complete dominance of *Saccharum spontaneum*. Strongly associated species were *Cynodon dactylon*, *Adenostemma lavenia*, *Ageratum conyzoides*, *Alternanthera sessilis*, and *Lippia nodiflora*. Two phases were distinguished.

MTG/Sasp/Sasp/Imcy (6a).--abundant *Imperata cylindrica* with cover from 10-100% indicated this phase. In most cases *Imperata cylindrica* and *Saccharum spontaneum* were codominants. This phase occurred predominantly as a mosaic in response to apparent micro-relief and micro-soil patterns in recent floodplains, or as heavily cropped grazing lawns or pastures (Fig. 14). Prostrate *Imperata cylindrica*, *Chrysopogon asciculatus*, *Eragrostis* spp., and *Cynodon dactylon* were common on heavily grazed sites and pastures. *Saccharum spontaneum* persisted at a low density in heavily grazed locations.

MTG/Sasp/Sasp/Sasp (6b).--nearly complete dominance by *Saccharum spontaneum* indicated this type. Associated shrubs such as *Artemisia indica* and *Triumfetta rhomboides*, and *Trewia nudiflora* seedlings were few and with low cover.

MTG/Sasp/Phka (7).--*Phragmites karka*, *Typha elephantina*, and *Narenga porphorycoma*, along with *Saccharum spontaneum* indicated this marsh association. Standing water is present for most of the year at these locations. Associated species were *Saccharum arundinacea*, *Cyperus* sp., *Persicaria* spp., and the fern *Dryopteris* sp..

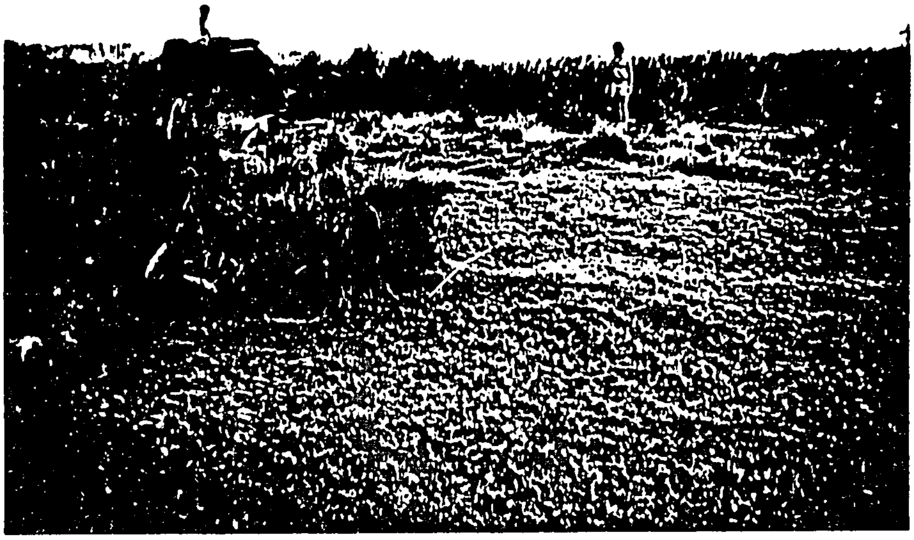

Fig. 14. A natural "grazing lawn" formed primarily by rhinoceros grazing in *Saccharum spontaneum* (tall grass in background) and *Imperata cylindrica* (shorter, 1 m grass) grassland (*top*); and, a similar village pasture (*bottom*). Exclosure on pasture was used for production studies; *Imperata cylindrica* emerged as the dominant grass with protection from grazing.

Saccharum bengalense-Shrub (SS) with *S. spontaneum* Associations

Saccharum spontaneum was codominant with *Saccharum bengalense* in these associations. *Artemisia indica* was a shrub indicator. *Saccharum spontaneum* generally had a cover value of greater than 33%. Other strongly associated species were the grasses *Apluda mutica* and *Imperata cylindrica*, the shrubs *Zizyphus mauritania*, *Colebrookea oppositifolia*, *Callicarpa macrophylla*, and the liana *Acacia rugosa*.

SS/Sasp types were further divided into two weakly different associations based on the presence or absence of the indicator *Artemisia indica* (Arin).

SS/Sasp/Arin (8).-- the association was indicated by 10-33% cover of *Artemisia indica*, with a similar cover of *Saccharum bengalense* and *Saccharum spontaneum*. *Callicarpa macrophylla* and *Acacia rugosa* were also strongly associated with this type.

SS/Sasp/Sabe (9).--near complete *Saccharum bengalense* dominance and a scarcity of *Artemisia indica* and *Saccharum spontaneum* characterized this association. Absence of *Saccharum spontaneum* may seem odd given the use of Sasp in the name, but other species were common between the two associations (8 and 9), especially *Zizyphus mauritania*. *Phragmites karka* was also a strong associate species.

Saccharum bengalense-Shrub (SS) with *N. porphorycoma* Associations

SS/*Narenga porphorycoma* types were characterized by a strong codominant or subdominant role of *Narenga porphorycoma* with *Saccharum bengalense*. The type was indicated by *Narenga porphorycoma* and *Saccharum arundinacea*. *Arundo donax* and *Narenga fallax* were very strongly associated grass species. Associated shrub species were *Desmodium gangeticum*, *Grewia sclerophylla*, and the liana *Vallaris solanaceae.* Soils were generally Entisols that probably were somewhat more developed than SS/Sasp habitats.

SS/Napo/Sabe (10).--the association was indicated by *Saccharum bengalense* codominance with *N.porphorycoma,* and the presence of *Clerodendron viscosum. Colebrookea oppositifolia* and *Pogostemon benghalensis* were strong associates.

SS/Napo/Nafa (11).--*Narenga fallax* as a subdominant species indicated this type. Shrub species were very poorly represented in these plots. This association was similar to the Mtg/Napo/Sabe associations (4a, 4b).

Riverine Forest Types

Trewia-Bombax riverine forests (12).--*Trewia-Bombax* riverine forest was indicated by the presence of *Murraya koenigii,* and strong associations with the grasses *Arundo donax, Cynodon dactylon, Oplismenus compositus,* the shrubs *Clerodendron viscosum, Colebrookea oppositifolia, Pogostemon benghalensis, Acacia rugosa, Vallaris solanaceae,* and the trees *Litsea monopetala, Bauhinia malabarica* and *Bridelia retusa.* Common overstory tree regeneration are *Bombax ceiba, Trewia nudiflora, Litsea monopetala, Mallotus philippinensis, Ehretia laevis,* and *Premna obtusifolia.* Other overstory species that are fairly common are *Albizia* spp., *Cassia fistula, Bischofia javanica, Acacia catechu,* and *Dalbergia sissoo. Coffea benghalensis* is a common understory shrub in some stands that were not sampled.

Mixed riverine forest (13).--mixed riverine forest indicator species were the shrubs *Murraya paniculata,* and *Persea duthiei,* a sparse cover of the grasses *Narenga porphorycoma* and *Saccharum bengalense* near the grassland ecotone, and the trees *Persea* sp. and *Mallotus philippinensis.* Dominant overstory species found in this forest are *Bombax ceiba*, *Persea* sp., *Dysoxylum* sp., *Trewia nudiflora*, *Mallotus philippinensis*, and *Ficus racemosa*.

Mixed riverine forest occupies the oldest and most well-drained upland sites, and is a later successional phase of the *Trewia-Bombax* riverine forests. The relative age of mixed forests is indicated by many old channel cuts on the margins of the stands, and by a well-developed evergreen tree component, compared to the earlier successional *Trewia-Bombax* riverine forest on obviously newer terraces. Elements of incipient mixed riverine forest can be found in the *Trewia-Bombax* riverine forest as regeneration and understory plants; remnants of *Trewia-Bombax* riverine forest species, such as *Bombax ceiba*, can be found in the Mixed riverine forest, in which evergreen species appear to dominate and regenerate under their own canopy.

GRADIENT ANALYSIS

Detrended correspondence analysis was performed on the same dataset of 146 species used for classification. Four ordination gradients were calculated with eigenvalues of 0.465, 0.366, 0.227, and 0.130. Gradient lengths were 4.14, 3.27, 3.91, and 2.18 standard deviations. The first and the third gradient lengths were greater than or nearly equal to 4.0, indicating a likely complete species turnover along these gradients (Gauch 1982). The first three gradients were used in the following analysis because the fourth seemed to contribute little to explaining the variation. Also, graphic illustration and analysis became complicated after three gradients.

A plot of the first two gradient axes shows a fairly even distribution of points in a triangular ordination space (Fig. 15). A contour diagram incorporating the first three ordination scores graphically illustrates plot separation along

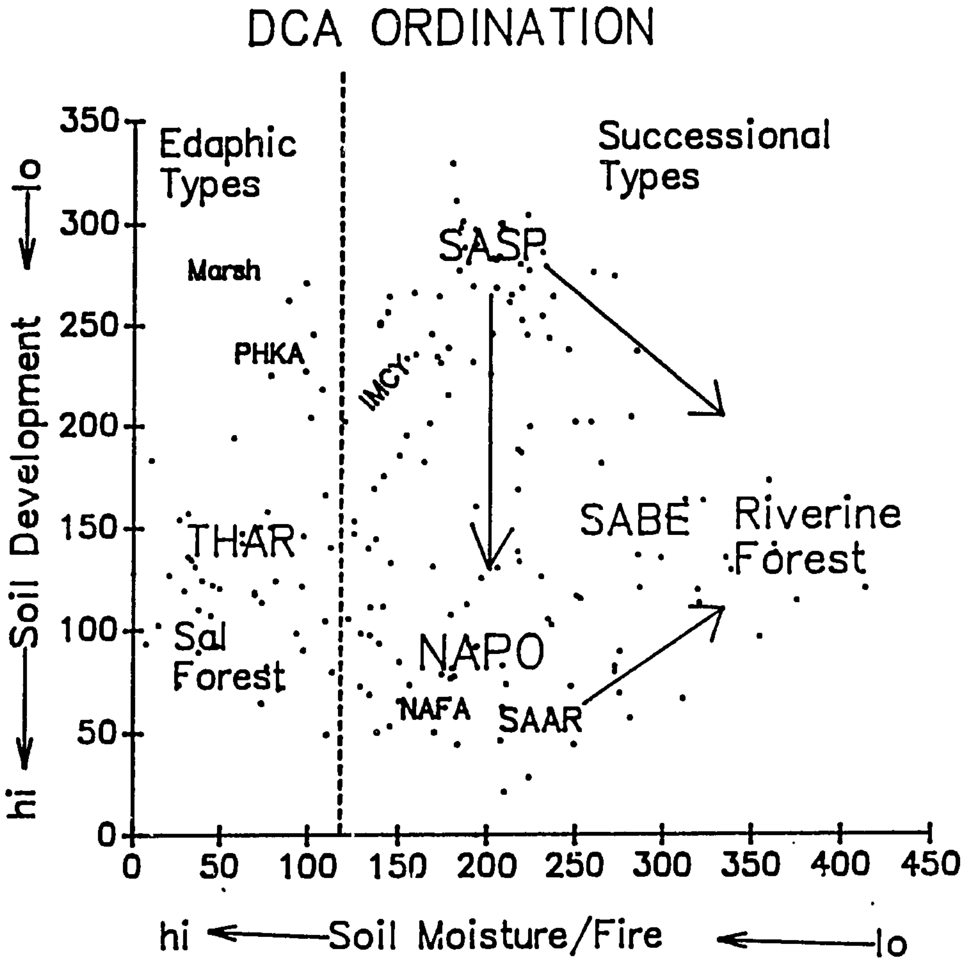

Fig. 15. Scatterplot of the first two ordination scores for community sample plots determined by detrended correspondence analysis (DECORANA). Rare species were downweighted in ordination. Axes are in standard deviation units x 100. Figure shows gradient interpretation of ordination space, and successional relationships (arrows). See Fig. 10 for species codes

three gradients (Fig. 16). The locations of the dominant grassland species across the ordination space can be discerned from the location of classified types (Fig. 15).

Saccharum spontaneum occurs primarily along the top right side of the space in types 6a, 6b and 9. *Saccharum bengalense* occurs mostly in the lower right quarter; it is about equally abundant in the Sabe/Shrub types 8-11, and in the MTG types 4a and 4b. *Saccharum arundinacea* and *Narenga fallax* are confined to the lower lobe of the space in types 4a and 11.

Themeda arundinacea occupies the lower left quarter of the space in types 2 through 3. *Imperata cylindrica* is found mainly in a broad band skirting the top of the "canyon" in the top left corner in types 2a, 2b and 6a. *Narenga porphorycoma* is a widespread and adaptable species found predominantly in the lower right quarter of the space, but common and abundant throughout the lower half of the ordination space.

The *Themeda* associations (1-4) occupy the topographic "peak" in the lower left corner, and the isolated peaks and transition zone at the base of the peak (Fig. 16). These sites are distinguished by an often high water table and residual basin or terrace soils older than the recent alluvial soils typical of sites to the right (Carson et. al. 1986), which are scattered over a gently rising plateau in ordination space. The marsh association (7), with *Typha elephantina* and *Cyperus* spp., occupies the topographic canyon in the top left corner. *Saccharum spontaneum* associations (6a, 6b) occupy the top of the ordination space. *Saccharum bengalense* associations (8-11) are found on the right half of the space. *Narenga porphorycoma* associations (4a, 4b, 5, 7) are located at the base of the peak on the "saddle" that runs along the base of the *Themeda* peak and the plateau.

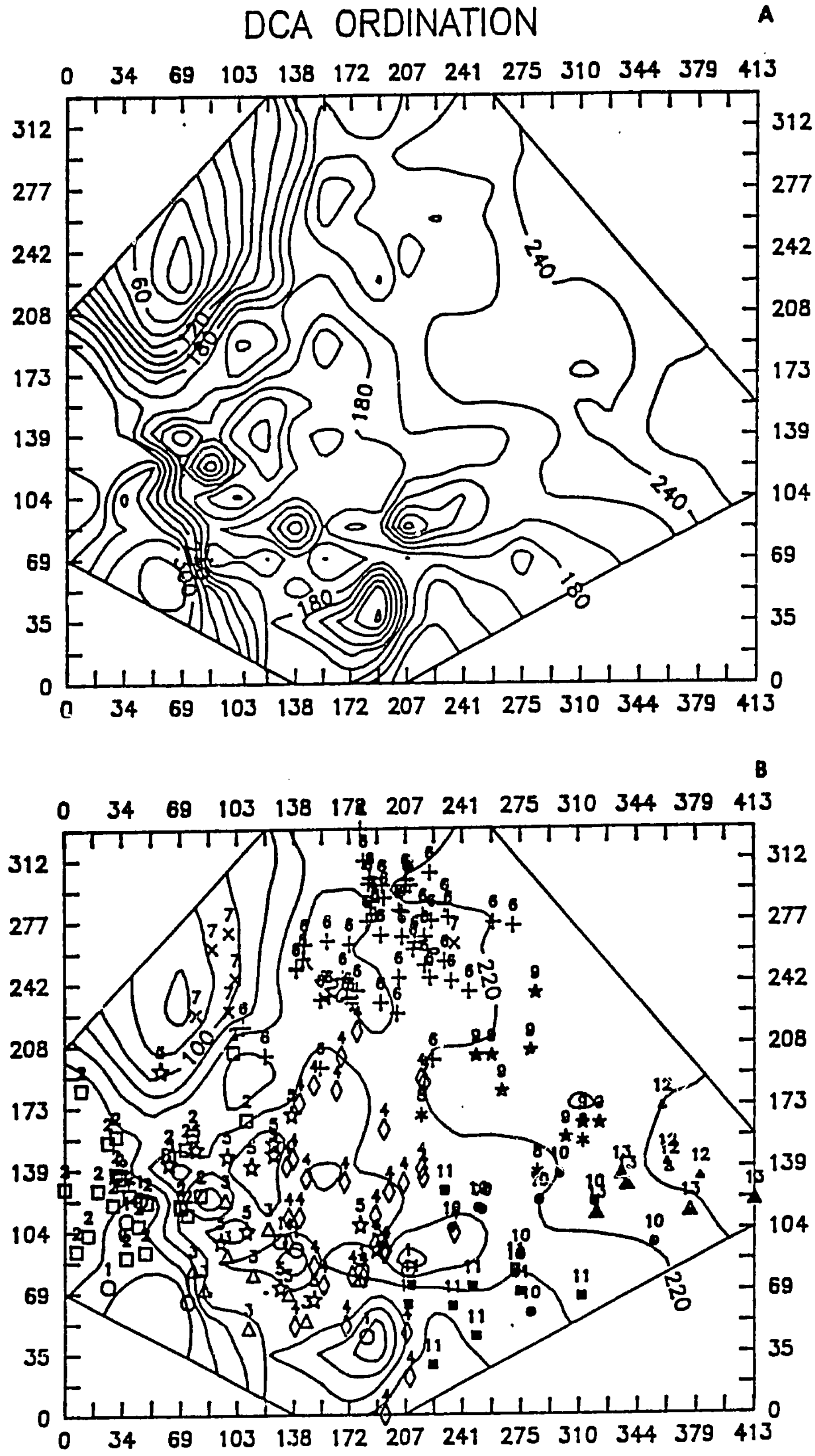

Fig. 16. Contour diagrams of the first three ordination scores for community sample plots determined by detrended correspondence analysis. A) Contour plot with 20-unit contour lines, without sample locations posted; and, B) with contour lines of 40-unit intervals and sample plots locations posted in ordination space. Type numbers are as given in Fig. 10.

The first gradient can be explained best as an increasing shrub gradient indicative of interacting soil moisture and disturbance gradients, with fire as the principal disturbance. Associations on sandy-loam soils with good drainage occur on the right side of the gradient (Fig. 16). Woody plants thrive on these soils. Litter accumulation and the herbaceous ground cover are low; litter decomposition is rapid during the monsoon, and the deciduous nature of many shrubs reduces above-ground fuel. Fire intensity is low and has little effect on the understory.

Progressively wetter soils occur down the gradient, conditions are poorer for woody plants, and grass dominance increases. Most sample plots fell near the center of the gradient, where there is an transition from *S. bengalense*–Shrub types on the right to grassland associations on the left. High grass and low shrub cover lead to a positive feedback system; high grass cover provides abundant fuel from ground level to several meters above the ground, which results in hotter fires and higher shrub mortality, than where shrubs reduce fine fuels. Grasses continue to dominate these sites. Fire effects are a gradient, however, because of variation in fire occurrence and intensity across the landscape. Fire has relatively greater effects on the left, high soil moisture parts of the gradient because of the low shrub cover; i.e., the interactive effect is a proportionally higher susceptibility of fire damage to shrubs on sites with high soil moisture, and a longer time to succeed to riverine forest.

Interpretation of the first gradient is somewhat confounded by the presence of sal forest at the wet end of the gradient, because sal requires well-drained soils. I think this end of the gradient is best explained as the location for plots where soil conditions limit shrub cover in some way, either by a high water table (grassland and marsh associations), or, droughty conditions caused by excessive stoniness or low porosity (sal forest). These soils are the oldest in the study area; nutrient levels or other conditions peculiar to these soils may further influence the plant associations.

Samples on the left side of the first gradient were then separated on another soil moisture gradient along the third (z) axis. The majority of the samples show similar levels of soil moisture on this gradient, as indicated by the broad topographic plateau in the right two-thirds of the ordination space (Fig. 16). The end points of the gradient are occupied by dry sal forest (1) near the "peak", and wet marshes (7) in the "canyon" at top left (Fig. 16).

Saccharum spontaneum types (6a,6b) on recent alluvium, at the top of the ordination space, anchor one end of a time gradient reflecting a soil development gradient (y axis). The majority of the sample plots are found at the lower end of the gradient on the more developed soils of older terraces. Sal forest plots on the oldest soils are all near the bottom of this gradient.

To examine successional dynamics in ordination space, segregate sal forest (1), associated grass types 2a, 2b, and 3, and marsh (7) from the left side of the ordination space, as relatively stable edaphic associations, by drawing a line, from the tic mark at 120 on the abscissa, parallel to the ordinate in Figure 15. A triangular-shaped successional space results with the imaginary drawn-line as the base, and riverine forest at the apex, to the right side of the x axis.

Succession might proceed as follows. *Saccharum spontaneum* associations colonize recent alluvium. Succession would take these sites on a trajectory down the top side of the triangle to riverine forest. However, fire retards horizontal movement toward riverine forest, deflecting the successional trajectory vertically down the soil development gradient. Soil development, primarily increased nutrient availability with the accumulation of organic matter and allogenic input from flooding and other sources, allows the establishment of other species that require less severe soil nutrient and moisture conditions. The first of these species would be *Saccharum bengalense*, and later *Narenga porphorycoma*, *Narenga fallax*, and *Saccharum arundinacea*. It also may be the case that these species arrive at the site later.

As a result of concurrent soil development and fire, MTG associations become established. Their successional trajectory to riverine forest is along the lower side of the triangle. Fire continues to retard this movement, but cannot prevent the succession entirely because of stochastic variation in intensity and occurrence.

Livestock, domestic elephant, and wildlife grazing, and fodder cutting for domestic animals add to the disturbance effects of fire. Wild grazers and elephants will eat seedlings of woody species in grassland. Elephant handlers cut and remove *Bombax ceiba* saplings growing within the clumps of tall grass cut for elephant fodder, and also limb small (less than 15 m) *Bombax ceiba* trees for fodder.

SUCCESSION EXPERIMENTS

Succession on Sand Bars

Periodic inspection of the sand bar exclosure through March 1986, revealed no growth of any grasses from seeds that had been planted earlier. All nodes of *Saccharum spontaneum* sown on the surface and planted 5 cm below the surface died.

Heavy rain showers fell from early April through late May; then there was a brief dry spell until the monsoon rains began about 15 June. Floods threatened the exclosure during the first week of July, so I ended the experiment on 8 July 1986.

The effect of the April rains on growth of planted and unplanted *Saccharum spontaneum* was remarkable. By July, the exclosure was lush with vigorous *Saccharum spontaneum* plants. Plants grew in all plots and between plots, regardless of previous treatment. I measured the height and number of stolons from a random sample of 30 clumps: mean height was 1.5 m (± 0.16; $p=.05$), and mean number of stolons was 21.8 (± 5.9; $p=05$). Stolons were up to 2.5 m long. Plants of other grass species were not found inside the exclosure.

Outside the exclosure the apparent density of stems was similar to inside the exclosure, but stem height on a random sample of 70 clumps averaged only 16 cm (± 2.2; $p=.05$), cover was very sparse, and few plants had stolons. The mean depth of the crown top under the sand surface was 3.6 cm (±.8; $p=.05$); 97% of the stems appeared to come from buried seeds. Tillers that arose from stem pieces were buried an average of 12 cm below the surface, where capillary action from the high water table probably kept the soil moist.

Elephants relish the new growth of *Saccharum spontaneum*, especially the stolons, and handlers often graze the elephants on these sandbars at the end of the day or when their grazing time is limited. Grazing had almost completely eliminated new growth of *Saccharum spontaneum* on these accessible sandbars. I had hypothesized that grazing stimulated stolon growth and production, and, therefore, elephants facilitated colonization of sandbars and to an extent their own food supplies. Grazed plants had very little stolon growth, and did not appear to compensate for grazing by increased growth rates or stolon growth.

Succession in *Imperata cylindrica* Swards

The number of live *Narenga porphorycoma* and *Saccharum spontaneum* stems plot^{-1} was significantly different between species and treatments (with and without *Imperata cylindrica*), but a significant species x treatment interaction was detected (Table 2). Single-species comparisons for treatment effects showed that the presence of *Imperata cylindrica* had a significant negative effect on *Saccharum spontaneum* stem survivorship but not on *Narenga porphorycoma*. Survival of *Narenga porphorycoma* stems was very low and probably a result of poor planting survival.

The presence of *Imperata cylindrica* significantly decreased the total live dry weight per plot of tall grass tillers planted in *Imperata cylindrica* (Table 3). *Saccharum spontaneum* and *Narenga porphorycoma* were significantly different in their growth response; *Saccharum spontaneum* yielded much more live biomass than *Narenga porphorycoma*.

However, *Saccharum spontaneum* stems are typically much more dense than *Narenga porphorycoma* stems, and may have been heavier at the beginning of the experiment. Pre-planting stem weight was unfortunately not measured, which precluded analysis of initial stem weight covariance. As an alternative, live biomass production per live stem was subjected to analysis of variance. No significant difference was detected in mean live dry weight stem-1 between species or treatments (Table 4). I concluded that the effect of Imperata cylindrica on tall grass was primarily on stem survival and not on growth rates.

Table 2. Cell means for number of live stems of *Saccharum spontaneum* (SASP) and *Narenga porphorycoma* (NAPO) in presence and absence of *Imperata cylindrica* (IMCY). Species differences significant ($p \leq 0.001$), but treatment effect significant for SASP only ($p \leq 0.001$). Different superscripts indicate significant differences.

	no IMCY	IMCY		
NAPO	4.8	4.0	=	8.8^{a}
SASP	17.6^{c}	10.6^{d}	=	28.2^{b}
Total	22.4	14.6		

Interaction: $p \leq .05$

Table 3. Cell means for live dry weight (g) of *Saccharum spontaneum* (SASP) and *Narenga porphorycoma* (NAPO) tillers in presence and absence of *Imperata cylindrica* (IMCY). Means were obtained from back-transformation of square-root transformed mean. Treatment and species differences significant at $p \leq 0.05$ indicated by different superscript.

	no IMCY	IMCY		
NAPO	14.6	5.2	=	19.8^{a}
SASP	44.9	32.5	=	77.4^{b}
Total	59.5^{c}	37.7^{d}		

Interaction: ns

Table 4. Cell means for live dry weight (g) per live stem for *Saccharum spontaneum* (SASP) and *Narenga porphorycoma* (NAPO) tillers in presence or absence of *Imperata cylindrica* (IMCY). No significant differences detected.

	no IMCY	IMCY		
NAPO	3.3	1.7	=	5.0
SASP	2.7	3.3	=	6.0
Total	6.0	5.0		

Interaction: ns

DISCUSSION

LANDSCAPE DYNAMICS

System Behavior

I hypothesized that the landscape would be in dynamic equilibrium, or a "shifting mosaic" (Bormann and Likens 1979; Heinselman 1981). Analysis of landscape change from aerial photographs and modeling of landscape dynamics suggested that the landscape is not at equilibrium. Real changes in the area and distribution of habitat types were observed over time from aerial photographs.

Much of the short-term dynamics of the landscape were initiated by abandonment of agricultural land. The effects of succession on these lands was diminished after about 30 years as most of the area succeeded to relatively stable, tall-grass and woodland associations from Imperata cylindrica. Agriculture was a one-time perturbation (sensu White and Pickett 1985) initiating secondary on developed soils succession in a manner unlike relatively frequent fluvial disturbance, which initiates a more primary succession on young floodplain soils.

Landscape dynamics uninfluenced by humans perturbation and under a semi-natural disturbance regime can be inferred from model system dynamics beyond the 30-year effect of agricultural succession. By semi-natural I mean that human intervention in landscape dynamics is pervasive and cannot be divorced from a "natural" disturbance regime. Humans influence flooding through deforestation in the hills, and upland processes by annual grass cutting and intentional burning. The importance of these anthropogenic disturbances will be discussed shortly, but in terms of landscape dynamics they are frequent, and probably permanent, variables of system dynamics.

Long-term dynamics were not stable (Fig 7B). Model simulations indicated a rapidly increasing *Saccharum spontaneum* floodplain habitat, and slow increases in other habitat types. Increase of the *Saccharum spontaneum* type was largely caused by a slow rate of succession to mixed tall grass types relative to input from the floodplain. The distribution of non-*Saccharum* types became relatively stable after 100 years (from 1964), but the absolute area continued to increase from erosion of agricultural lands outside the Park into the floodplain.

Model Evaluation

Assumptions of the linear landscape model are spatial homogeneity of processes, linearity of rates, deterministic successional change, and realistic system boundaries. Stable landscapes assume similar properties (White and Pickett 1985): uniformity of patch distributions over time; feedback between community characteristics and disturbance (linearity); stable disturbance regimes and predictable successional states (determinism); small patch size relative to the landscape unit; and an invariable patch size class distribution. The linear donor-controlled model would appear to be a good paradigm to model shifting mosaics and their response to perturbation. However, many of the assumptions of the linear model, and shifting mosaic theory, have questionable application to Chitwan grasslands.

Spatial Homogeneity.--spatial homogeneity assumes that model processes are uniform over the modeled area. The most serious deviation was in assuming spatial homogeneity of fluvial processes, primarily channel changes and bank scouring. All locations in the study area do not have an equal probability of being influenced by river action, as type patches are not evenly distributed over the landscape. Although a particular problem in modeling corridors such as river floodplains, this assumption would likely be a problem in modeling patchy landscapes with a high amount of disturbance, unless patchiness was explicitly modeled.

Succession rates would be much less subject to spatial bias than fluvial processes. However, spatial variation could be produced by variability in soils, and the extent and intensity of disturbances, such as fire, grazing, and grass cutting. Soil conditions vary within the gross types used in the model, primarily by age, which equates to soil development or increased availability of soil resources, and elevation from the water table.

Fire distribution is uniform over the landscape, as nearly all the area burns during late January and early February. Some areas escape burning until spring; but, very few sites remain unburned by May. However, my experience and that of others (Loucks et.al. 1985; Gillon 1983) is that fire intensity varies with air temperature and relative humidity, which depend on the time of day and season.

Wild animal grazing is comparatively consistent for selected habitats over the landscape throughout the year. Herbivores are resident species, unlike the large migratory herds of East Africa (McNaughton 1977, 1979a; Cumming 1982). Domestic elephant grazing is non-uniform, with areas closest to the stables more heavily grazed and cut over for fodder. Illegal livestock grazing is primarily confined to a strip no more than .5 km wide along the Park boundary.

Species composition of the general model types used in the model, and, thus, patch interactions, vary considerably. The mixed tall grass type encompasses associations dominated by *Saccharum bengalense*, or *Narenga porphorycoma*, or a mixture of these species with *Narenga fallax*, *Saccharum arundinaceum*, and *Saccharum spontaneum*. Small grazing lawn inclusions also occur. These variations were impossible to identify with black-and-white aerial photographs at 1:35,000 scale. Patch size, shape, and distance from propagable sources varies, and will influence successional transitions (Pickett 1976; Pickett et. al. 1987).

Rate Linearity.-- Linearity assumes that the rate of change is a function of area and a constant rate parameter, i.e., an exponential function. This is the paradigm for linear donor-controlled models as used in landscape succession models (Bledsoe and Van Dyne 1971; Shugart et. al. 1973; Weinstein and Shugart 1983; Shugart and Urban 1986). Discrete-time matrix (Raedetzke and Van Dyne 1976, 1979; Swartzman and Singh 1974) and Markov models (Hool 1966; Horn 1976; Van Hulst 1979; Usher 198), also have been widely used to model succession. Matrix models also assume linear or stationary rates (Shugart et. al. 1973), but transition parameters are in probabilistic form (Swartzman and Kaluzny 1987).

Succession is arguably nonlinear and stochastic. Debate on this question has centered around the use of Markov models to model succession. Markov models assume that transfer rates are stationary, and that system conditions at time *t+1* are a function only of conditions at time *t* (Van Hulst 1979; Usher 1981). The history of the site is assumed to have no bearing on the future condition, that the emergent properties of the type are expressed in the vegetation (Van Hulst 1979; Usher 1981).

Markov and linear models assume a Clementsian (1916) deterministic perspective of step-wise succession, whereas nonlinear, stochastic approaches embody the Gleasonian (1926) individualistic approach (Van Hulst 1979). Contemporary thinking on succession has rejected the deterministic view of succession, and promoted individualistic explanations (Egler 1954; Drury and Nesbit 1973; Connell and Slatyer 1977; Tilman 1985; among others). This calls to question the validity of using linear models of succession.

Empirical evidence against the validity of Markovian assumptions is inconclusive, but theory hedges toward rejection of the model (Van Hulst 1979; Peet and Christensen 1980; Usher 1981; but see Lippe et. al. 1985). Nevertheless, the utility of linear succession models resides in their simplicity and value for prediction (Usher 1981), their heuristic value, and statistical properties which allow testing for stationarity (Van Hulst 1979). Simplicity, however, is deceptive, because the construction of meaningful transition matrices is not trivial (Usher 1981). Loucks et. al. (1985) suggested that linear compartment models of succession have potential to predict secondary succession. Calibration of the model successional rates for transitions not influenced by river action was minor, suggesting little deviation from linearity.

Rate parameters associated with floodplain processes required substantial calibration. This suggests that fluvial processes are non-linear and stochastic. The amount and timing of precipitation, and resulting flooding severity, vary between years. There is a popular notion, which is perhaps unsubstantiated (Carson et. al. 1986), that flooding severity is increasing in the Himalayan river systems due to increasing deforestation and erosion. This would cause the rate parameters that include erosion processes to increase. River channel changes are a function of flooding severity and topographic variation, and are not linear or deterministic processes. Other types of disturbance, fire and grazing for example, may introduce additional nonlinearity into the system.

Independence of transition rates and system topology from site history is a weak assumption (Usher 1981). Site conditions may vary across landscapes and influence the trajectory of succession. The spatial distribution of species will influence colonization, species distributions, and competitive relations at a site. Disturbances, such as fire and grazing, may alter species relationships, and change system topology. For example, fire in Chitwan may contribute to a deterministic change in successional stages by retarding woody succession until late successional grass species dominate the site. The next stages can only be woodland, then riverine forest. If fire was absent, woodland could form from earlier grassland associations, and cause branching in successional topology.

System Boundaries.-- Expanding the boundaries of the model system beyond the study area may influence model behavior. A bottleneck in the floodplain occurs at the eastern upstream side of the study area. Above the bottleneck, the floodplain is wide and straight with a braided channel. Downstream the channel constricts and makes a wide S-curve near Sauraha, and remains relatively narrow and channeled along the remainder of the 30 km to its confluence with the larger Narayani River.

The bottleneck forces the braided channel into one entity, increasing the force and speed of the current. About one km downstream, a smaller but substantial stream, the Kagari Khola, adds force and volume to the river. These are the forces likely responsible for the extensive mosaic of grassland and riverine forests below the bottleneck in the Sauraha study area, which are the most extensive in the Park.

The consequence of modeling this active area of the river is to limit the generality of the model. A much larger area should be modeled to account for the high variability of floodplains, and accurately represent system behavior.

Model Predictions

What good are the model predictions, given the problems associated with non-linearity, stochastic processes, and boundary limitations? Also, independent data for corroboration of model behavior was not available. The model was intended only as a preliminary examination of system behavior (Swartzman and Kaluzny 1987), primarily to aid management and identify topics for research, which will be discussed later. I think the model has met these simple objectives. Trends in succession of upland types not affected by river action may have been reasonably modeled, as described earlier with regard to rate linearity.

Short-term floodplain changes in habitats and erosion are less predictable than for upland types because fluvial processes are stochastic. However, some trends are evident, and are likely to continue over the next 10 years. There has been a considerable increase in the amount of the *Saccharum spontaneum* type since 1981 that conforms to model behavior. Additional increases in floodplain *Saccharum spontaneum* are likely, because the channel configuration indicates continued steady erosion of agricultural and forest lands along the Park boundary. River bank stabilization in agricultural areas would only dampen the increase rate of the *Saccharum spontaneum* type, but not change the upward trajectory (Fig. 9). Only a major straightening and channelization of the river or major flood would alter the predicted trajectory. The volatile nature of sub-Himalayan river action is a natural phenomenon that cannot be easily altered by human action (Carson et.al. 1986).

The simulation of fire effects was approximate at best. The model structure did not allow an explicit modeling of fire effects. Moreover, there was little data to guide modification of the rate parameters to test hypotheses of fire effects. A further problem with the method is that fire could change the topology, or transitions from state to state, as described earlier. The simulations represented the boundaries of a plausible system response within the model topology, and point to an area of needed research.

CLASSIFICATION

The grassland classification reproduced patterns observed in ordination space, and grouped sample plots into an ecologically meaningful gradient that indicated an edaphic or successional status based on shrub cover (Fig. 10). The arrangement reproduced the first gradient of the ordination, because the correspondence analysis used in gradient analysis is a detrended form of reciprocal averaging used in TWINSPAN (Gauch 1982).

The proposed classification differs markedly from that proposed by Dabadghao and Shankarnarayan (abbr. D&S) (1973). The D&S *Phragmites-Saccharum-Imperata* is a very generalized type (Yadava and Singh 1977) that would appear to have very limited value in Chitwan for classifying grassland types and explaining community organization.

The *Phragmites-Saccharum-Imperata* type seems to correspond rather well to the Mtg/Sasp/Phka marsh type. Both have similar species composition and are relatively stable edaphic types. However, the single D&S type fails to account for the majority of types found in Chitwan, and does not satisfactorily explain primary or secondary succession under a natural disturbance regime. However, their scenario of succession under intense livestock grazing, fodder cutting, and burning reasonably describes some responses of the Chitwan types to heavy disturbance. Their scheme rather simplifies the process, however.

Intense human disturbance in most all the grassland types results in dominance of *Imperata cylindrica*. *Imperata cylindrica* is widespread throughout the area, occurring to some extent in nearly all the sample plots. Abandoned agricultural land was rapidly colonized by *Imperata cylindrica* (Bolton 1975), and was shown to succeed to Thar/Napo and Mtg/Napo types.

Intense grazing and cutting of *Saccharum spontaneum* and *Saccharum bengalense*-shrub types results in a similar dominance of *Imperata cylindrica*. Evidence of this was in the short-cropped, natural grazing lawns classified as a Mtg/Sasp/Imcy phase, and in studies of protected village pastures (Chapter III). *Saccharum spontaneum* was a suppressed component of pastures, and responded readily to protection by growing to full height in one season (Chapter III).

Heavily grazed sites, such as pastures, had a large component of prostrate, grazing resistant, perennial and annual grasses such as *Chrysopogon asciculatus*, *Cynodon dactylon*, *Sporobolus* spp., and *Eragrostis* spp. (Chapter III) as suggested by D&S.

SUCCESSION

Theoretical Background

Successional theory has moved in the direction of a reductionist approach, emphasizing disturbance, life history characteristics of species, and competitive relations rather than a Clementsian deterministic progression to climax (Peet and Christensen 1980). An apparent dichotomy of theory exists in addressing the importance of progressive soil development and availability of soil resources as a possible cause of succession.

Many of the life history approaches (Drury and Nesbit 1973; Horn 1974; Werner 1976; Pickett 1976; Van Hulst 1978; Glenn-Levin 1980; Noble and Slatyer 1980; among others) discount the importance of soil development, or soil resource availability, as a possible cause of species change. Other authors explicitly address soil development, along with life history and disturbance, as possible causes of succession (Egler 1954; McCormick 1968; Connell and Slatyer 1977; Tilman 1985, 1988; Huston and Smith 1987; among others). It seems that this dichotomy stems from a failure to separate the cause (soil development) and mechanism (colonization, competition, etc.) in theory (Pickett et. al. 1987), and that both approaches are valid depending on the circumstances.

Life history alone would appear most useful in explaining secondary succession where soil resources are adequate and little changed by disturbance. The soil resources and life history approach would be appropriate for understanding primary succession, or secondary succession where soil resources are poor. This flexible approach was adopted by Tilman (1985, 1988) in his resource-ratio theory, and will guide the following discussion.

Primary Succession

Primary succession on new floodplain soils begins with rapid colonization by *Saccharum spontaneum*. Colonization ability is a function of seed dispersal at the end of the monsoon, and propagation from detached stem nodes (Bor 1960). The sandbar experiment and sampling of crown depths suggested that burial in sediment positions seeds to germinate and grow in response to pre-monsoon showers in April.

Buried stem nodes appear to be secondary sources of colonization. Nodes experimentally placed on the sand surface and nodes buried 5 cm below the surface rapidly desiccated. Poor survivorship could have been a result of experimental selection and handling of stem pieces; but, I think it more likely that nodes were too exposed to survive. Crowns of plants outside the experimental area arising from buried nodes were few and were buried nearly 5 times deeper than crowns arising from seed, where soil was likely moister.

Seeds of late-successional wind-dispersed grasses, *Saccharum bengalense*, *Narenga porphorycoma*, and *Imperata cylindrica* that were experimentally sown on the sandbar did not germinate. I could not determine if *Saccharum spontaneum* seeds sown on the surface germinated, because the use of contaminated sand resulted in uncontrolled growth of *Saccharum spontaneum* in the exclosure. Crown depths of *Saccharum spontaneum* tillers outside the exclosure indicated that seeds and nodes germinated about 4 cm and 12 cm below the surface. However, it is possible that the plants had become established on the surface, and wind later buried the crowns.

Seeds from the late-successional species must settle very near the sand surface, and their subsequent germination may be inhibited. Very little is known of the factors affecting germination of C_4 grasses; but high light intensity, low soil moisture, and surface temperature in excess of 40° C inhibit germination (Jones 1985). Although exposure to white light is necessary for germination, prolonged exposure to high white light intensity can inhibit germination, the "high irradiance reaction" (Frankland 1981; Toole 1973). Light inhibition may be an adaptation to prevent germination where strong sunlight may desiccate seedlings before roots can reach moist soil (Jones 1985). The effects of light can vary with species (Lahiri and Kharabanda 1964), ecotypes (Cole 1977), and with duration of after-ripening period and inhibition temperature (Voigt 1973). Germination can be inhibited by soil temperatures greater than 40°C (Jones 1985).

Soil temperatures during April on production plots in *Saccharum spontaneum* grassland peaked at 37°C (Chapter III); the soil surface on these plots was partially shaded so that it is reasonable to assume that temperature on exposed sandbars exceeded 37°C. Percent moisture of a 25 cm soil column on the same plots was about 0.5% during April and rose to about 1% during May (Chapter III). Buried *Saccharum spontaneum* seeds may escape light inhibition, but more importantly are located where temperatures may not be excessive, and where germinating seeds may avoid desiccation after dry season showers until roots are established in soil moistened by capillary action from the high water table.

Information on germination of sugarcane (*Saccharum officinarum*) seed that might clarify the effects of the environment is difficult to find in the literature, because nearly all sugarcane is planted from stem "setts", or node sections (Kakde 1985). Germination of seeds is considered too variable and unpredictable for agriculture.

Saccharum spontaneum associations were found primarily in nearly pure stands on sandy floodplains (types 6a, 6b), but also in a wide range of environmental conditions from marshes with *Phragmites karka* and *Typha elephantina* (type 7) to more well-drained MTG stands. Marshes have standing water for most of the year; floodplains have sandy soils with good drainage and droughty conditions during the dry season when the water table drops.

The occurrence of *Saccharum spontaneum* in the two extremes of soil drainage would be puzzling if not for the fact that *Saccharum spontaneum* is known to have wide genotypic variation (Jones 1985). Dillewjin (1952) cites examples of Indian varieties growing on sites with water up to 1.5 m deep for five months. Typical varieties of sugarcane can survive extremely wet conditions for extended periods of time, and some varieties are selected to grow on saturated soils (Jones 1985). Yield for most varieties, however, is reduced under extremely wet conditions for extended periods, or even by periodic flooding (Juang and Uehara 1971; Gumbs and Simpson 1981; Escolar and Allison 1976).

Saccharum spontaneum swards on well drained soils in Chitwan appeared more vigorous than stands on poorly drained sites. Another contributing factor may be that soil nitrogen availability is similar on recent alluvium, with a low initial stock, and in waterlogged soils where nitrogen mineralization is low (Tilman 1985) and nitrification losses are high (Donahue et. al. 1977).

Later Transitions

Interpretation of sample plot locations in ordination space suggested that successional dynamics beyond the *Saccharum spontaneum* colonization stage are a function of time and increasing availability of soil resources (y axis), and disturbance and soil moisture (x axis). Fire and herbivory, the primary disturbances, had observable and the predictable effects of maintaining grass associations by delaying woody succession (Vogle 1974; Daubenmire 1968; Gillon 1983; Cole 1986; among others) to riverine forest. Schmid (1958, 1974; in Blasco 1983) described a very similar "edaphic climax", alluvial grassland-savanna in Vietnam that is maintained by fire. Dominant species are the familiar grasses *Narenga porphorycoma, Phragmites karka,* and *Echinochloa* spp., with trees and shrubs from the genera *Albizzia, Clerodendron, Dillenia, Emblica, Grewia, Zyzyphus,* and *Terminalia.* A few more words will be said about fire later.

Soil moisture is recognized as one of the primary determinants of grassland and savanna organization (Smeins and Olson 1970; Bazzaz and Parrish 1981; Sarmiento 1983; Tinley 1983; Cole 1986; among others). Measurements were not taken that could confirm the hypothecated soil moisture gradient, but field observations and the position of woody and grass species on the ordination axis suggested that soil moisture formed a complex gradient with disturbance.

Shrubs would be expected at the dry end of the gradient because they are much less tolerant of poor drainage than grasses (Michelmore 1939; Tinley 1983; Knoop and Walker 1985; Walker et. al. 1981). Woody plants would further amplify the moisture gradient by their action as transpiration pumps keeping the water table low and enhancing soil drainage (Tinley 1983). A positive feedback loop is established whereby better drainage favors establishment of woody plants over grasses, which increase soil drying from transpiration loses, which encourages woody species (Walker et. al. 1981; Knoop and Walker 1985). Marsh and Thar/Napo/Imcy associations, known to be edaphic associations on waterlogged soils, occurred at the opposite end of the gradient from shrubs.

I have no empirical evidence to indicate that soil development, or an increase of nitrogen availability, usually the most limiting soil nutrient for plants (Donahue et. al. 1977; Tilman 1988), occurs over time during primary succession in Chitwan's alluvial soils. Soil maps and chemical analysis data are available for the Chitwan valley but the resolution is too course to be useful. Robertson et. al. (1988)reported a high degree of small-scale variation on the order of 1 to 40 m in old-field nitrogen availability, which was related to topographic variation in soil moisture. This relationship likely occurs in Chitwan, rendering current maps useless at the scale of this research.

Increasing nutrient availability with time is generally considered the norm (Donahue et. al. 1977; Tilman 1985, 1988; Huston and Smith 1988; but see Drury and Nesbit 1973 for disagreement), particularly for incipient soils in primary succession. Opinions diverge on whether allogenic or autogenic processes are primarily responsible. This cuts to the heart of the succession controversy; autogenic succession indicates a facilitation model of succession (facilitation could take other forms, however), whereas allogenic succession dictates population or life history explanations of succession (Huston and Smith 1988; Tilman 1985).

Both allogenic and autogenic processes are probably important in Chitwan. Allochthonous nutrient input could be substantial. Sediment from periodic flooding of new and old floodplain terraces increases the stock of organic and inorganic nutrients. Allogenic succession based on sediment deposition during monsoon rains has been described by Misra (1946). High insolation and soil temperature, and good aeration of these porous soils allows high nitrogen mineralization rates (Donahue et. al. 1977). Input from pre-monsoon thunderstorms and monsoon rains is another source (Donahue et. al. 1977). These are probably the reasons why Carson et. al. (1986) said that alluvial soils are the most productive in Nepal.

Autogenic processes are present, but their effectiveness is hard to assess. Normally, nutrient availability will increase with incorporation of organic matter from litter (Donahue et. al. 1977). Litter accumulation in Chitwan grasslands is low, however, because of annual fires. Large amounts of nutrients are lost with fire through volatilization (Daubenmire 1968; Vogle 1974; Gillon 1983); but, increased mineralization from high post-fire surface temperatures results in a net increase in available nitrogen (Daubenmire 1964; Vogle 1974; Wright and Bailey 1982; Hulbert 1988; James 1988; among others). Fire also increases nitrogen availability from precipitation by eliminating litter and standing dead material, and the microbial action in this material, that intercepts and removes nitrogen from the system (Seastedt 1985). Substantial organic matter input as a result of fire is realized by root and crown mortality and incomplete combustion of litter and dead material (Vogle 1974; James 1988); enough that Vogle (1974) claimed that burning is the primary factor in the development of rich North American prairie soils.

The flooding and ruin of the experiment to test the facilitation hypothesis of *Saccharum spontaneum* to *Saccharum bengalense* succession was disappointing. Interpretation of such experiments, as proposed by Connell and Slatyer (1977) to test their models, may be ambiguous anyway (Quinn and Dunham 1983; Pickett et. al. 1987). However, some observations can be forwarded in support of several succession hypotheses.

Saccharum bengalense is uncommon on *Saccharum spontaneum* grassland less than three years old, indicating poor seed dispersal, improper conditions for germination, or a need for moderate soil development. *Saccharum bengalense* seeds are plumed for air-born dispersal, but winds are uncommon during December when dispersal occurs, and seed dispersal is probably limited. In this case, the life history of dispersal would constrain succession to *Saccharum bengalense.*

Saccharum bengalense germination could be inhibited by direct strong sunlight or high surface temperatures, as discussed earlier. The presence of pioneer *Saccharum spontaneum*, which thrives under those conditions, would facilitate *Saccharum bengalense* establishment by shading the ground and providing favorable light, soil moisture, and soil temperature conditions for germination. Several years growth of *Saccharum spontaneum* on new sandbars may also provide the necessary organic matter required for *Saccharum bengalense* establishment.

Saccharum bengalense is common on rhinoceros latrines in *Saccharum spontaneum* grassland with otherwise little *Saccharum bengalense.* This indicates better *Saccharum bengalense* establishment on sites with higher organic matter and nutrient status than on recent alluvium, and supports the hypothesis of a soil development gradient, but not necessarily facilitation.

Ordination suggested that *Narenga porphorycoma* was most abundant on wetter and more developed soils, in the sense of more organic matter, than those favorable to *Saccharum bengalense*. The model for transition to *Narenga porphorycoma* types, therefore, is probably "tolerance" (McCormick 1968; Connell and Slatyer 1977) constrained by life history of dispersal. Transition to *Narenga porphorycoma* associations could happen under two possible circumstances.

Fluvial action on the landscape is variable, and wet depressions with high silt deposits are sometimes created adjacent to steep banks. *Narenga porphorycoma* was observed to dominate such sites. *Narenga* seed dispersal would appear poor based on the absence of plumes and high winds during December seed dispersal, and *Saccharum spontaneum* would initially dominate such depressions by nature of its rapid colonizing ability. Favorable soil nutrient and moisture conditions would favor later germination and establishment of *Narenga porphorycoma* as a superior competitor for light, once seeds reached the site. In this case, dispersal ability constrained establishment of *Narenga porphorycoma*.

The second scenario under which *Narenga porphorycoma* becomes established is through succession to a mixed tall grass association with *Saccharum spontaneum* and *Saccharum bengalense*. Interpretation of the ordination suggested such a transition under the influence of disturbance, primarily fire. Fire would retard succession to riverine forest from *Saccharum bengalense* associations, and concurrent soil development would increase nutrient and moisture (Kellman 1985) availability and allow *Narenga porphorycoma* to become established. Mixed tall grass associations would then succeed to riverine forest slowly under the influence of the disturbance gradient.

Secondary Succession

The experiment on succession from *Imperata cylindrica* to *Saccharum spontaneum* and *Narenga porphorycoma* was partially successful. Inhibition of *Saccharum spontaneum* by *Imperata cylindrica* was demonstrated by increased mortality of *Saccharum* stems planted within an intact *Imperata* sward. Stem mortality of *Narenga porphorycoma* with *Imperata* was not significantly different, however; poor transplanting success with *Narenga* was the probable reason for this result.

Imperata cylindrica is known to be a very competitive weedy species (Hubbard et. al 1944; Eussen and Wirjahardja 1973; among others), one of the world's ten worst weeds (Holm 1969; Holm et. al. 1977). Eussen (1979) observed depressed yield of maize and sorghum, but no effect on *Imperata cylindrica*, in replacement series competition experiments. Studies by Kushawa et. al. (1983) and Eussen and Niemann (1981) suggested that allelopathic properties of leaves were partly responsible for the high competitive ability of *Imperata cylindrica*.

My field observations suggest that *Saccharum* and *Narenga* invade *Imperata* swards mainly by lateral spread. *Saccharum spontaneum* spreads rapidly on sandbars from stolons and rhizomes (Bor 1960); *Narenga* also has a stout rhizome and is considered a good soil binder (Bor 1960). Established tall grasses would provide a photosynthetic source for lateral and underground stems, and weaken nearby *Imperata cylindrica* by shading. *Imperata cylindrica* is known to be very susceptible to shading and invasion by fire resistant tall grasses and herbs (Hubbard et. al 1944; Eussen and Wirjahardja 1973; Falvey and Hengmichai 1979; Saxena and Ramakhrishnan 1983). Lateral vegetative propagation of dominant late-successional perennials has been reported as the predominant mode of recolonizing disturbed areas in North American tall-grass prairies after cessation of heavy grazing (Glenn-Lewin 1980), and in East Africa on small physically disturbed patches (Belsky 1986b, 1986c, 1986d). Some propagation of tall grass by seed is indicated by the presence of isolated clumps of *Saccharum* and *Narenga*. These plants presumably became established in gaps in the *Imperata* sward. Grass cutting and burning may promote tall establishment by exposing the ground surface to sunlight and reducing competition. The increase in soil surface temperature during fire is negligible 1 cm below ground (unpub. data), and would not damage seed pools (Daubenmire 1968; Vogle 1974). Large mammals, such as wild boar, may facilitate grass invasion by disturbing the soil and creating gaps.

DISTURBANCE

Fire

Fire was proposed in the gradient analysis as retarding succession to riverine forest. My observations indicate, however, that fire may play an opposite role of encouraging woody succession.

I noted that the understory of my unburned mixed tall grass experimental production plots was much more depauperate than the burned plots. Dead leaves on unburned plots formed a very dense mat about 1 m above the ground. Very little light reached the ground, and few woody plants were present.

I proposed the hypothesis for model simulations that fire enhances woody succession by removing dead material and litter, and allowing light to reach the ground surface. Woody plants would become established in burned areas, and could escape damage or be destroyed by later fires through random variations in fire occurrence and intensity. Fire suppression would slow succession to riverine forest by inhibiting tree regeneration. Inevitable fires from careless humans, lightning, or even spontaneous combustion in damp areas (Vogle 1974) would be intense as a result of high fuel loads and inflict greater damage to existing trees than cooler annual fires.

Herbivores

Large mammalian herbivores affected the grassland community primarily as regulators of system processes (Chew 1975; Lee and Inman 1975; MacMahon 1981; McNaughton et. al. 1982; Dyer et. al. 1982; Belsky 1987b), rather than consumers (Cumming 1982; McNaughton 1985). Consumption was estimated roughly as only 6-10% of net aerial grassland production (Chapter III). Herbivore effects on community organization were not detected in gradient analysis and appear small relative to soil moisture and nutrient gradients, fluvial action, and fire. This is in contrast to the significant impact of large mammalian herbivores in East African grassland ecosystems (McNaughton 1983; Cumming 1984; Belsky 1986b).

Rhinoceros, the dominant wild herbivore, affect landscape patterns and processes in a number of ways. Scattered small grazing lawns (McNaughton 1984), less than .25 ha, are created by heavy cropping of *Imperata cylindrica* patches on the *Saccharum spontaneum* floodplain. A few sample plots fell of these lawns; but, they were classified as the MTG/Sasp/Sasp/Imcy phase, which also included ungrazed *Imperata cylindrica* stands. Lawns provide foci of high quality forage by nature of new growth, and an area of colonization for annual grasses and forbs. Rhinoceros influence the structure of the riverine forest communities by selectively browsing saplings of the trees *Litsea monopetala*, and to a lesser extent *Mallotus philippinensis* and *Dalbergia sissoo* (E. Dinerstein, unpublished manuscript).

Rhinoceros are primary dispersers of seeds from the tree *Trewia nudiflora* (Dinerstein and Wemmer 1988). After ingesting the fruit in riverine forest, rhinoceros disperse the seeds in grassland, principally in floodplain *Saccharum spontaneum* grassland. Germination is enhanced by the rhinoceros behavior of defecating in communal latrines, which provide a nutrient-rich seedbed. Rhinoceros also disperse a number of other herbaceous riverine forest and grassland species that become established at latrine sites (E. Dinerstein, unpublished manuscript). Latrines also provide humus-rich foci for establishment of wind-dispersed *Saccharum bengalense* on recent alluvium dominated by *Saccharum spontaneum*, thereby facilitating succession to *Saccharum bengalense* dominated associations.

Domestic elephants are the direct or indirect cause of many changes in the landscape. Each of nearly 40 elephants requires the cutting of about 65 kg DW grass per day, and consumes 25 kg DW grass daily while grazing (Chapter III). Tall grasses do not compensate for biomass removal (McNaughton 1985b; Dyer et. al. 1982; Hilbert et. al. 1981; Belsky 1986a) and resulting openings in the canopy enable herbaceous understory species to thrive. Limbs of the pioneer savanna tree, *Bombax ceiba*, account for 10% of the diet; an average 116 kg of limbs are cut per elephant meal. The limbed skeletons of young *Bombax ceiba* trees are common throughout the grassland-riverine forest mosaic within several kilometers of the elephant stables. Young trees are selected because of the high proportion of edible bark on new limbs that are easily accessible by climbing. Saplings are also cut inadvertently by handlers cutting fodder. Elephants also browse the common grassland pioneer trees, *Acacia catechu, Dalbergia sissoo, Bauhinia malabarica*, and browse on the common climber *Acacia rugata*.

Smaller herbivores add to disturbance. While grubbing for worms and insects, wild boar uproot tall grasses and create small (a few square meters) to medium (about 100 m^2) sized gaps in the grassland that could be colonized by ruderal species, which are widespread in Chitwan, or riverine forest trees and shrubs. However, Belsky (1986b, c, d) found that similar disturbances by large mammals in Kenya had little impact on the grassland mosaic where ruderal species were few; patches were revegetated by adjacent perennial grasses in Kenya, not by annuals or ruderal species. Boar rooting also may aerate soil, and increase litter and subsequent humus, as does the burrowing of prairie dogs in North America (Collins and Barber 1985). Hog deer disperse the seeds of the common grassland pioneer tree *Xeromphis uliginosa.* Axis deer and sambar are other dispersal agents of *Trewia nudiflora* seeds in floodplain grasslands (Dinerstein, unpublished manuscript).

Extirpated large herbivores, wild buffalo, swamp deer, and wild elephant, likely played important roles in seed dispersal (Dinerstein and Wemmer 1988) and as disturbance agents (Seidensticker 1976).

SUMMARY

Landscape dynamics of the grassland-riverine forest mosaic in the 27 km^2 study area, from Sauraha to Dumaria, were examined with a simple linear donor-controlled model. The structure of the model was based on a theoretical sequence of landscape succession, because specific successional transitions could not be determined from aerial photographs due to the long time period between photograph years. The model was intended only as a preliminary exploration of landscape dynamics; some model assumptions may not hold for this highly dynamic system. Aerial photographs from 1964 and 1981 were used to calculate parameters of landscape change.

The river was the focus of landscape dynamics: erosion, deposition, and channel meandering destroyed, created, and modified habitats constantly. During the 17-year period between photograph years, river channel area increased 56%. Floodplain sandbars increased 215% inside the Park, and 121% outside the Park. The landscape was not stable, or a "shifting mosaic", with constant properties. Analysis of the photographs and model simulations indicated that three subsystems of landscape change existed in the dynamics

One subsystem consisted of the river channel, and lands outside the Park that are influenced by river action. About 45 ha of agricultural and 52 ha of forest land were eroded into the river during the 17-year period, an average of 5.7 ha $year^{-1}$. The net loss of outside-Park lands was only 22 ha, because some of the lost upland remained in floodplain habitats outside the Park.

The floodplain and upland habitat inside the Park was the main landscape subsystem. This subsystem displayed dynamics different than outside the Park, because the river channel was primarily cutting outside lands and depositing on the Park side of the river. These habitats made up the majority of the study area. *Saccharum spontaneum* floodplain habitat increased 73% since 1964 to become the most abundant vegetation type. Model simulations show that *Saccharum spontaneum* habitat area will double over the next 50 years, if current trends continue and dominate the landscape. The area will continue to increase rapidly or the next 200 years if model assumptions are correct, which may not be the case for the simple model. The increase in *Saccharum spontaneum* habitat was a consequence of faster creation of floodplain habitat than succession to mixed tall grass habitat.

The third landscape subsystem consisted of reclaimed agricultural land succeeding to natural vegetation. About 540 ha of wet paddy fields succeeded primarily to a stable mosaic of *Narenga porphorycoma*, *Themeda arundinacea*, and *Imperata cylindrica*. Another 309 ha of dry fields reverted to savanna and woodland in mosaic with *Imperata cylindrica*. *Imperata cylindrica* dominated these lands in nearly pure swards after they were reclaimed; but, after 25 years nearly all have disappeared under tall grass. It was estimated that 66% of the area will revert to tall grass within 10 years.

Ten grassland associations, with 6 phases, and three forest associations were identified from 188 sample plots of the study area. Types were classified on an edaphic and successional gradient indicated by the amount of shrub cover. *Themeda* and *Narenga* dominated types occurred on the wettest sites with the smallest shrub cover, and appeared to relatively stable over time. The majority of types, with *Saccharum spontaneum* and *Saccharum bengalense*, but also some with *Narenga porphorycoma* were considered stages in succession to riverine forest.

Fluvial action was the controlling force of community organization at the landscape level. At the next level of organization, the among-habitats level), indirect gradient analysis suggested that soil moisture, soil development, and fire were the primary gradients underlying community organization and succession. Succession was discussed as a complex function of species life history characteristics and population processes, and increasing soil resources over time. Large mammalian herbivore feeding and fodder cutting for domestic elephants were secondary factors. Herbivores were felt to be most important as agents of site disturbance and plant dispersal, and regulators of community organization, rather than consumers. Only 6-10% of aerial net primary productivity was consumed by large mammalian herbivores.

CHAPTER III. FIRE, GRAZING AND PRIMARY PRODUCTION

INTRODUCTION

Sub-Himalayan alluvial grasslands are potentially the most productive in the world. Production estimates for four north Indian grasslands were higher than estimates for 48 of the 52 temperate and tropical grasslands reported by Coupland (1979). The height of these Indian grasslands is generally less than 2 m (Misra 1979); whereas, sub-Himalayan grasslands of the general *Phragmites-Saccharum-Imperata* type (Dabadghao and Shankarnarayan 1973) reach heights of 4-7 m. Based on the relative height differences, one might infer a much greater productivity of *Phragmites-Saccharum-Imperata* grasslands.

Indian productivity research reviewed by Yadava and Singh (1977), Coupland (1979), and Misra (1979) has overlooked the productive, sub-humid *Phragmites-Saccharum-Imperata* grasslands at the base of the Himalaya. Past studies have concentrated on the dryer *Dicanthium-Cenchrus-Lasiurus* and *Sehima-Dicanthium* types found to the south or west. Floristically, the dryer grassland types are similar to other monsoonal Asian and Australian, and African grassland savannas at the generic level: characteristic genera are *Dicanthium*, *Bothriachloa*, *Chrysopogon*, *Eragrostis*, *Heteropogon*, and *Themeda* among others (Beard 1967). Human disturbance in the form of heavy livestock grazing and burning are considered the principle factors in the establishment and maintenance of these Indian grasslands (Champion 1936; Puri 1960; Dabadghao and Shankarnarayan 1973).

Sub-Himalayan grasslands of the general *Phragmites-Saccharum-Imperata* type are found on alluvial landscapes, where fluvial action, poor drainage and fire maintain a dynamic mosaic of edaphic and successional tall grass savanna and riverine forest types (Chapter II). *Phragmites-Saccharum-Imperata* grasslands occur throughout northern India in the Gangeatic plain on low-lying and poorly drained alluvial soils (Dabadghao and Shankarnarayan 1973). However, the vegetation of these areas is much more complex than indicated by a single name. I classified ten grassland types and 6 phases from the Chitwan National Park. These can be reduced in terms of structure, growth habit and productivity into tall-grass *Saccharum spontaneum* swards, mixed tall grass swards with *Narenga porphorycoma*, *Saccharum bengalense*, and *Themeda arundinacea*, and short *Imperata cylindrica* swards. Similar types were described by Schmid (1958, 1974; in Blasco 1983) in Vietnam.

Very little has been productivity research has been done on the tall grasses, but a substantial literature exists on *Imperata cylindrica*, a pan-tropical weed (Hubbard et. al. 1944; Holm 1969; Holm et. al. 1977). The paucity of research on tall Indian grasslands may be explained by the difficulties of working on tropical floodplains, and the fact that most of the Gangeatic plain is under cultivation.

PRODUCTIVITY OF CHITWAN GRASSES

Abiotic Factors

The basic factors in the high productivity of Chitwan grasslands are alluvial soils and high year-round soil moisture availability (Chapter II). Alluvial soils are characterized by high allochthonous inputs of organic matter in flood sediments, high mineralization rates as a result of good aeration and porous structure (Donahue et. al. 1977), and high cation exchange capacity and base exchange (Carson et. al. 1986). These soils are the most productive in Nepal, and the predominant soil in the "breadbasket of Nepal" Terai region (Carson et. al. 1986).

The growing season begins during late January after burning. Nearly all the grassland area is burned by thatch cutters. Average daily temperature begins to rise from a low of 15°C during January (Fig. 4). Growth is steady through the dry season despite the lack of rain, and then appears to increase rapidly with the onset of monsoon during June. Growth ceases about late September with the end of the rains and the rapid drop in average daily temperature from 27°C. *Saccharum spontaneum* is the first to flower in late September; *Saccharum bengalense* and *Narenga porphorycoma*, among other grasses on more well-drained sites, flower during the early part of the cool, dry season from early November through early December.

Fire Effects

Fire has been assumed an important influence throughout the evolutionary history of grasslands worldwide (Daubenmire 1968; Vogle 1974), and particularly in south Asia where the climax vegetation is said to be forest (Puri 1960; Wharton 1968; Blasco 1983). Fire effects on production depend on many variables, such as intensity, timing, fuel loads, and frequency (Daubenmire 1968; Vogle 1974; Gillon 1983). Production and forage palatability are usually higher after fire, but production response depends on the season and species (Kucera and Ehrenreich 1962; Daubenmire 1968; Old 1969; Vogle 1974; Abrams et. al 1986).

Fires in Chitwan's recent past have been wholly anthropogenic, and nearly always started early in the dry season during late January or early February (Bolton 1975). Natural fires, however, would occur late in the dry season during April, when convection storms sweep the area. Natural fires usually have a different frequency, intensity, and effect than anthropogenic fires (Gillon 1983). Early season fires generally stimulate production, but late season fires usually depress production (see references in Daubenmire 1968; Vogle 1974; and Gillon 1983). Grasses burned in January or early February in Chitwan have already grown substantially by April; if unburned grasses follow a similar phenology, late season fires would likely reduce production. However, production on unburned sites is likely to start later than on burned areas, where the absence of litter results in high soil temperatures and early production (Daubenmire 1968; Vogle 1974). The question is what effects would late burning in Chitwan have on production, and what might the evolutionary implications be?

Tropical grasses are notoriously poor in nutrient quality during mature stages (Van Soest 1982). However, fresh regrowth initiated after fire is high in protein, and is an important forage for herbivores during the dry season when forage quality is lowest (Daubenmire 1968; Lemon 1968; Vogle 1974; Allen et. al. 1976; Gillon 1983; Christensen 1977). If large ungulate populations (domestic and wild) are limited by nutrient or resource availability (Klein 1970; Sinclair 1975; Clutton-Brock et al. 1982; McNaughton 1983), the role of fire in the dynamics of forage quantity and quality will be important for understanding the regulation of ungulate populations and their management.

Grazing Effects

Grazing can also influence the quality and quantity of above-ground grass biomass. Grazing will usually reduce the standing crop of biomass (Heady 1975; Crawley 1983), and often reduce total annual productivity (Jameson 1963; Younger 1972; Dyer et al. 1982; Belsky 1986a). However, some research has suggested that grass productivity is sometimes higher with moderate grazing than with lower or higher intensities of grazing (McNaughton 1979a, b; Dyer et al. 1982; McNaughton 1985a, b). Regrowth after grazing is also of higher quality than ungrazed forage

(Christensen 1977; Reuss et. al. 1983; McNaughton and Chapin 1985; McNaughton 1985b). The result is a higher grazing capacity. The interactive effects of grazing and fire on grass production and quality have significant impacts on energy and nutrient cycling (McNaughton et al. 1982; McNaughton 1985b), and ecosystem productivity (Van Dyne et. al. 1980).

With the exception of the *Saccharum spontaneum* floodplain grasslands, most grasses show little evidence of grazing. *Narenga porphorycoma* and *Saccharum bengalense* swards are apparently grazed slightly for several months after fire, but appear tall, dense, and ungrazed throughout the remainder of the growth cycle. Herbivore density in most of these swards is very low (Mishra 1982a). However, herbivore density in the general grassland-riverine forest mosaic has been reported as the highest in south Asia and among the highest in the world (Eisenberg and Seidensticker 1976; Seidensticker 1976). The questions are: How much of the productivity is removed? When is it consumed? How might quality affect consumption?

Studies of grass production and quality, in conjunction with concurrent studies of herbivore food habits conducted by other ecologists, will yield significant insight into the structure of the herbivore community (Demment and Van Soest 1986), the population dynamics of grassland herbivores (Caughley 1976a), and herbivore reproductive and foraging strategies (Belovsky 1984, 1986; Owen-Smith and Novellie 1982).

HUMAN USE

Management of the grass cutting program is a primary concern of Park managers. The contribution of grass products from the Park to the local village and household economies is approximately NR 10 million ($500,000) (Mishra 1982b).

There is an increasing demand for Park resources with local population growth (Sharma 1986).

Fodder resources for village cattle are in short supply in the areas surrounding the Park (Sharma 1986). Supplies are particularly low during the hot dry season from March through May, and many people sneak into the Park to cut grass or let their cattle wander into the Park to graze. Most cattle return the same day, but many are impounded by Park guards or are eaten by tigers. The cow is the national animal and it is a crime to kill a cow or sell one for slaughter; so, impounding cattle and collecting fines from people who cannot or will not pay is a problem (Mishra 1982b). Cattle-killing tigers deprive villagers of their primary means of work energy and a substantial investment. Strategies to manage thatch grass inside the Park and to increase fodder supplies outside the Park are necessary to reduce conflicts with villagers (Mishra 1982b, 1984; Sharma 1986).

Crop depredation by wildlife is a grave problem for villagers living adjacent to the Park (Milton and Binney 1980; Mishra 1982b, 1984). Fences and trenches have been tried with little success for various natural and sociological reasons (Mishra 1982b). One solution may be to manage grassland production with fire or mechanical means to increase Park forage supplies during the peak growing seasons.

The questions for research are how much grass is removed illegally by villagers for subsistence living, what is the value of these products to the local economy and the individual village family, and what might the impacts be on wildlife?

OBJECTIVES AND HYPOTHESES

The objectives of the primary production studies are to: 1) Examine the effects of fire and wildlife grazing on aerial net primary production (ANPP) and annual herbage dynamics in three major grassland types: *Saccharum spontaneum*, *Narenga porphorycoma*, and *Imperata cylindrica*; 2) Determine the ANPP of a village pasture and the effects of grazing intensity on production; 3) Examine long-term grass biomass production, consumption, and availability in the study area by coupling a production model with a model of landscape dynamics (Chapter II); 4) Consider ways to manage grass resources inside and outside the Park to meet the needs of conservation and local village development.

There are several hypotheses that the research proposes to examine:

Hypothesis: Aerial net primary productivity (ANPP) is among the highest in the world.

Hypothesis: Early dry season (January) burning increases ANPP by reducing dead material causing an increase in insolation and soil temperature and the stimulation of growth.

Hypothesis: Late dry season (May) burning, which simulates a natural burning regime, occurs after the growing season has begun and will reduce production relative to early burning.

Hypothesis: Grazed pasture grasses do not overcompensate for grazing by producing more than ungrazed grasses, i.e., there is no grazing optimization.

Hypothesis: Grazing on natural grazing lawns and village pastures increases species diversity, but lowers primary production.

Hypothesis: Large herbivores remove less than 10% of primary production, and have little impact on the productivity of the grassland system.

METHODS

FIRE AND GRAZING EFFECTS ON ANPP

Study Areas & Experimental Design

Three experimental sites were selected in homogeneous stands of *Imperata cylindrica*, *Saccharum spontaneum*, and *Narenga porphorycoma*. The *Narenga* site, which contained some *Saccharum spontaneum*, was meant to be representative of a "mixed tall grass" (MTG) type (Chapter II). MTG swards are usually dominated by *Narenga* with lesser amounts of *Saccharum bengalense*, *Saccharum arundinacea*, and *Saccharum spontaneum* depending on soil moisture conditions (Chapter II). *Narenga* is the more widespread and common species, but *Saccharum bengalense* often codominates or dominates in some stands. *Narenga* and *Saccharum bengalense* are similar in phenology and morphology so that studies of *Narenga* fairly represent the dynamics of the mixed tall grass type.

Grazing treatments were grazed and ungrazed. Burn treatments were early burn (early February), late burn (mid-May), and no-burn. Each treatment combination was replicated twice with 20 m x 20 m plots in a randomized split-block design (Fig. 17). The 12 treatment plots were laid out in a 3 x 4 arrangement with each replicate consisting of a block of 6 plots. Plots were separated by a 5-m wide fire lane; a 10-m wide fire lane surrounded the entire site. Adjacent ungrazed plots for the two replicates were fenced with 5-strand electric fence powered by a 12-volt car battery. Project staff saw ample evidence that the fences were effective in repelling small (wild boar) and large (rhinoceros) herbivores. The split-block arrangement was used for convenience in fencing, to save scarce fencing materials, and reduce costs.

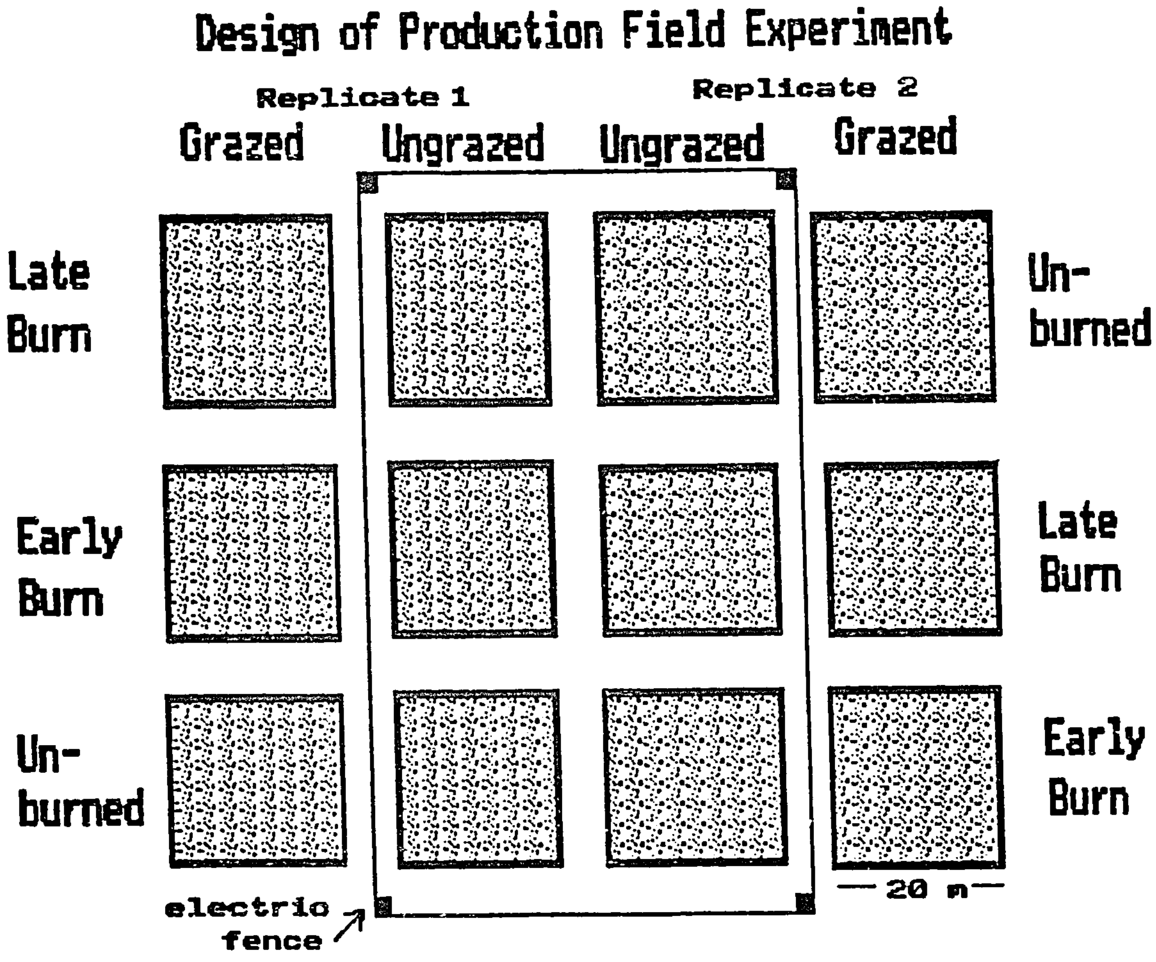

Fig. 17. Experimental design for randomized split-block field experiments to determine the effects of fire and wildlife grazing on aerial net primary production. Treatment plots were 20m x 20m separated by 5m-wide fire lanes.

Wire mesh cages 2 x 2 m in size were placed two each on the two replicate early-burn grazed plots to estimate aerial production (Milner and Hughes 1968) and forage removal (Lineham et. al. 1952). Cages were moved at each sample period until there was no apparent difference between inside and outside biomass, i.e., no evidence of grazing. This technique was used only on early-burn treatment plots because early burning is the prevalent practice. Also, grazing was insignificant or nonexistent on the unburned plots, and manpower did not allow similar treatment of the late burn plots. Cages were stolen from the *Saccharum spontaneum* site and replaced several times, after which their use there was discontinued.

Early burn plots were fired during the first week of February. Although most grassland in the Park burns 1 to 2 weeks earlier during the grass cutting season, it was impractical to burn our plots then because fire might have escaped the site and destroyed valuable thatch grass. Late burn plots were burned during mid-May. All burning was done by firing a plot's windward side. If accidental burning of adjacent plots was a threat, plots were fired from the lee side for a slower burn.

Approximate fire temperatures were measured with Tempilaq temperature sensitive paints painted on thin squares of sheet metal. Ceramic or other non-conductive materials were not available as media. The paints' temperature range spanned 66°–500°C. Painted squares were attached to green bamboo poles just below ground level, at ground level, and at 10, 30, 60, 100, 200, 300, 400, and 500 cm above ground level for the 2 tall grass types, but not above 100 cm on *Imperata cylindrica* plots. Ambient temperature, relative humidity, and wind speed were measured before each plot was burned. Elapsed time for burning the entire plot also was recorded.

Sampling began in early February 1986 and continued through February 1987 for all plots. Sampling continued on late burn plots through April 1987 to collect data for nearly a complete year. The late start of the entire project in April 1985, six months behind schedule and three months into the growing season, precluded starting the experiment during 1985 and collecting data for 2 full years.

Field Sampling

Biomass from sample quadrats on each treatment plot was clipped at 5-week intervals. One cutting period was skipped while I was in the United States during August 1986. Cutting was usually accomplished in 1 day, but rain often required a second trip to finish the work. Two 2.25 m^2 quadrats were clipped from each treatment plot and averaged to reduce within-plot variation of biomass production.

The 2.25 m^2 (1.5 x 1.5 m) clip plot size was determined by Wiegert's (1962) method. A larger quadrat size of about 4 m^2 was indicated as the optimum, but I felt that such a large quadrat was impractical. A frame was necessary because measuring and marking each plot was not feasible under the field conditions. Moreover, a 2 x 2 m plot frame would have been too unwieldy for transporting by elephant or carrying by hand, and for use in tall, extremely dense grass by relatively short people. Materials, such as PVC pipe, for building take-down frames were not available in the country. The 1.5 x 1.5 m frame was selected as a trade-off between optimum size and pragmatism.

Standing biomass was cut with sickles and placed in plastic garbage bags. Herbs were plucked or cut at ground level and bagged for identification and weighing. Litter was swept with brooms, weighed on site, and sampled from each quadrat for a combined sample. Litter from burned and unburned plots was kept separate depending on the height and density of the standing biomass.

Soil temperature was measured within the top 1 cm of soil with a dial thermometer on 1 plot from each treatment. Ten readings were taken about 1 m inside the north edge of the same plot during each consecutive sample period. Sometimes only five readings were taken if all five were within one or two degrees.

A soil moisture sample was taken from each plot with a soil sampling tube. The sample was a column 2.5 cm x 30.5 cm. Percent soil moisture was determined gravimetrically by drying at 100°C for 2 days.

Biomass Sorting and Subsampling

Cut samples were weighed immediately after arrival at camp. Cutting usually took all day to complete, so samples were stored in a covered area overnight. Samples were reweighed in the morning to get a "pre-sort" wet weight before sorting live from dead material.

Whole samples from mixed tall grass quadrats were sorted because the grass was course and dead material was easily separated from live. Samples from other plots were subsampled. Subsample weight was an *ad hoc* decision which depended on the fineness of the material: usually, 3 kg of *Saccharum spontaneum*, and 0.5-1.0 kg of *Imperata cylindrica* were sorted.

Live biomass from each quadrat was separated from dead leaves and stems, weighed, chopped, mixed, and 100 gm samples measured for dry weight estimation. Dead material from similar burn treatment plots was combined; a grab sample was chopped, and six 100 gm samples were measured for dry weight determination.

Litter was similarly handled. Herbs were identified and whole samples or subsamples were dried.

All dry weight samples were dried in the sun or on a rack over a wood cook fire until final drying in a lab oven at an agricultural college 10 km distant was possible. Drying was at 60--70°C for 2 days in a drafted laboratory oven.

Statistical Analysis

Live, dead, and live/dead dry weight ratios from each site and sample period were compared among treatments using Tukey's test (Sokal and Rohlf 1981); ratios that were not significantly different were pooled. Total live wet weight for each quadrat was determined by multiplying the pre-sort wet weight by the proportion of live biomass in the sort samples for that treatment, or for combined treatments. Live dry weight was calculated as the live wet weight times the live dry weight ratio. Dead dry weight was taken as the difference between live wet weight and pre-sort wet weight, times the dead dry weight ratio. Total dry weight was the sum of live and dead dry weights. Litter and herb dry weights were calculated as wet weight times the dry weight ratio. Litter was not used to calculate total weight based on the recommendations of Singh et. al. (1975); litter weight was typically low, quite variable and unavoidably contaminated with soil.

Full ANOVAs were done on dry weights for live and total weight. Residuals were examined for normality and heteroscedasticity by graphical methods (Tabchnick and Fidell 1983). I accepted a Type I error significance level of alpha=.1 as reasonable and acceptable for field experiments of this type.

ANOVA results were used when deciding whether to pool time series data of treatment biomass to determine aerial net primary productivity (ANPP). Live and dead biomass, but not litter, were used to estimate ANPP based on recommendations by Singh et. al. (1975) and Lauenroth et. al. (1986).

Statistical analyses were performed with the SYSTAT statistical analysis software for IBM-compatible personal computers.

Production Modeling

Primary production.--annual biomass production in the study area was estimated for all grassland types based on areas calculated by the succession model and production parameters determined by field studies. Production estimates assumed constant yearly production/unit area, and complete burning each year during late January or early February.

Production data collected in the field did not consider the complete array of consumers in the determination of net primary production. Particular attention was given to the availability and consumption of grass by domestic elephants, rhinoceros, and humans. Residual biomass after all consumption was estimated to assess available biomass for future uses.

Consumers.--consumption by rhinoceros, elephants, and humans was estimated by multiplying the number of animals or grass cutting permits by the per capita harvest. Production calculations for each grassland type were calculated as,

gross biomass = biomass/ha x area
net biomass = gross biomass - animal consumption
remaining biomass = net biomass - human consumption.

Population estimates of rhinoceros were calculated using 1975 census estimates (Laurie 1978) as an initial population size, and a minimum 2.6% annual increase estimated by Dinerstein (1985). An exponential rate of increase was assumed.

Rhinoceros per capita grass intake was estimated by the formula (Milner and Hughes 1968):

$$F = E \times I_e / I_f$$

where,

F = dry weight of forage intake per day

E = dry weight of excreta per day

I_e = proportion of acid detergent lignin in excreta

I_f = proportion of acid detergent lignin in forage

Acid detergent lignin (ADL) proportions were taken directly from Dinerstein (unpublished data) for excreta, and calculated indirectly for forage. Forage lignin was determined by taking an average of ADL for the ten most common forage species weighted by their relative proportion in the diet during October-November as determined by Gyawali (1986).

Weight of excreta was estimated by multiplying the daily defecation rate (Laurie 1978) times the average weight of defecation that I estimated during late October. Intake of grasses was calculated as 65% of the total annual diet as determined by Gyawali (1986).

The number of domestic elephants was constant during the two years of field research and is constant in the model. Their number is not likely to increase substantially. Elephant consumption rates were estimated by a year-long field study (this chapter). The weight and species of fodder cut for night feeding was measured, as was the amount actually consumed. Grazing intake was estimated by a bite-count technique. Total consumption of *Saccharum spontaneum* was calculated directly; total consumption in the Mixed Tall Grass and Woodland types was proportional to the area of the type.

Legal harvest rates of thatch and canes by grass cutters were estimated from field studies (this chapter). I assumed for the model that all grass from the *Themeda-Imperata* and *Imperata*-Agriculture types is cut for thatch. This thatch is a scarce resource in the entire district, and much sought after for personal use and resale. Cane harvest estimated from field studies was apportioned 25% to the *Saccharum spontaneum* type and the rest allocated to the Mixed Tall Grass and Woodland types (which have similar understories) in proportion to their area.

The number of grass cutting permits remained constant in the model; estimates during 1986 and 1987 were nearly the same, and are not likely to increase substantially unless more thatch grass is made available through management.

Illegal cutting of fodder during the hot season of February through May was roughly estimated for the *Saccharum spontaneum* cover type as 375 kg DW day^{-1}. No studies have been done to estimate illegal consumption of fodder, so I estimated conservatively that 25 loads per day are taken from the *Saccharum spontaneum* areas within the research area. I previously had estimated an average weight for grass loads of 35 kg, which when adjusted for 43% dry weight yields an average load weight of 15 kg dry weight.

PASTURE PRODUCTION

Production Measurement

A 22 x 22 m exclosure with a 5-wire electric fence was erected on a village pasture near the Park boundary. Standing biomass was clipped, then residual biomass scraped at ground level (to follow the method necessary outside the exclosure; see below) at 5-weekly intervals from 0.5 m^2 plots to estimate biomass production.

Biomass production outside the exclosure was measured by the caged-plot method with barbed wire exclosures. The grass was cropped so close by livestock that normal clipping with shears was impossible. We resorted to scalping the herbage not more than 1 cm below the ground, then washing the dirt away at camp. The dilemma with this procedure was that by scalping herbage just below ground we were getting more herbage than was available to livestock; but, clipping with scissors would not allow collecting all above ground biomass.

Livestock numbers grazing the pasture were counted within a day of clipping. This did not introduce serious error because the same livestock from the surrounding villages were consistently grazed in the same pastures.

Defoliation Experiment

An experiment was made inside the core of the exclosure to study the effects of four levels of defoliation intensity on production. Effects of defoliation every 11, 22, 45, and 90 days were compared to an undefoliated control. Six replicate 0.5 m^2 plots of each treatment were arranged in a randomized block design. Clipped biomass was bagged, dried at 60-70°C for 2 days, then weighed.

CONSUMPTION

Animal Consumption

Five elephants (4 adults, 1 immature) were available at the research camp for consumption studies. Elephant handlers collect grass fodder each morning for the elephants to eat at night. Cut fodder was weighed biweekly in the morning, and leftover fodder was weighed the next morning to estimate consumption. Grab samples for each sample were dried to estimate dry weights.

Elephants are taken to the jungle for 4-6 hours/day to graze under the control of a handler. I made separate observations of two different elephants at each biweekly sampling period to estimate intake by the bite-count technique. Elephants "pluck" a bit of forage, put it in their mouths, and when they get a mouthful take a "bite" and ingest the forage. The number of plucks per bite and the number of bites per 5-minute sample were counted for 15 samples.

I then collected grass similar to what the elephant had eaten to estimate bite weight. Bite weight was determined by estimating the number of stem or the amount of fine material observed in bites, weighing the material, and feeding it to the elephant. I recorded the amount eaten and discarded, if any. Samples were taken for dry weight estimation.

I measured the five elephants during the biweekly samples to discover if body condition changed during the year. Chest girth, neck girth, temporal gland diameter, ear-to-eye distance, and anal flap thickness were measured as suggested by C. Wemmer (National Zoo, pers. comm.).

Fodder species fed to the 33 government and five research elephants were determined from biweekly counts of fodder piles collected by handlers. Handlers also were questioned to determine in what grassland or forest types they were grazing the elephants.

Human Consumption

We counted the type and number of grass loads leaving the Park from the Sauraha entrance, one of the main entrances, from 1430 to 1800 hours each day during the legal grass cutting season. Loads were weighed from a random sample of grass cutters as they were leaving the Park, and at other locations inside the Park.

Visitation estimates from Sauraha and the total number of permits sold were used to estimate the total number of loads and amount of grass removed from the Park. We assumed that all permit holders came to cut grass on the first day, and used that as the denominator to first-day Sauraha visitation to estimate the proportion of cutters using the Sauraha exit. Estimates of total Park visitation on subsequent days were made by multiplying Sauraha visitation by the first day ratio. A questionnaire was administered to discover grass cutters' attitudes toward the Park. Complete details are found in Lehmkuhl et. al. (1988).

RESULTS

FIRE, GRAZING, AND ABOVEGROUND BIOMASS

Imperata cylindrica Grassland

I sampled only through January 1987, one month short of a year, because villagers cut grass from treatment plots outside the exclosure during the grass cutting season. I sampled the undamaged fenced plots to estimate ungrazed biomass production for the final tenth sample period, but this was not included in the ANOVA. Late-burn treatment plots were sampled through the end of April to estimate nearly a year's production from burning in early May the year before.

Analysis of variance was done on the total dry weight (live + dead standing material) and live dry weight (Table 5). Residuals appeared normally distributed in probability plots and tested normal with the Kolmogorov-Smirnov test. Plots of residuals and standardized residuals against estimated cell means did not show evidence of heteroscedasticity.

Table 5. Partial results of analysis of variance for *Imperata cylindrica* total dry weight and live dry weight biomass estimates in split-block grazing x fire experimental design. (*=$p \leq .1$; **=$p \leq .05$; ***=$p \leq 01$; ****=$p \leq .001$).

TOTAL DRY WEIGHT

Source of Variation	df	SS	MS	F	P
Samples					
Replicates	1	0.683	0.683		
Samples	8	27.216	3.402	28.367	0.000****
Error (S x R)	8	0.959	0.120		
Total	17	28.855			
Treatments					
Grazing	1	2.013	2.013	118.258	0.058*
Error (G x R)	1	0.017	0.017		
Burning	2	86.691	43.346	136.408	0.007***
Early vs late burn	1	1.622	1.622	5.101	0.152 ns
Early vs no burn	1	74.381	74.381	233.903	0.000****
Error (B x R)	2	0.636	0.318		
Grazing x Burning	2	0.682	0.341	2.290	0.304 ns
Error (G x B x R)	2	0.298	0.149		
Total	10	166.340			

LIVE DRY WEIGHT

Source of Variation	df	SS	MS	F	P
Samples					
Replicates	1	0.041	0.041		
Samples	8	9.680	1.210	26.461	0.000****
Error (S x R)	8	0.366	0.046		
Total	17	10.087			
Treatments					
Grazing	1	0.580	0.580	39.470	0.100*
Error (G x R)	1	0.015	0.015		
Burning	2	0.417	0.209	18.034	0.053*
Early vs late burn	1	0.027	0.027	2.250	$p>0.1$ ns
Early vs no burn	1	0.211	0.211	17.583	$p<0.1$*
Error (B x R)	2	0.023	0.012		
Grazing x Burning	2	0.276	0.138	8.005	0.111 ns
Error (G x B x R)	2	0.034	0.017		
Total	10	1.345			

Grazing and burning both had significant treatment effects. Total weight and live weight showed identical trends of significance in the ANOVA. Samples, or date of sampling, was considered a treatment, and not surprisingly showed a significant difference over the year.

Grazing Treatments.--a slight grazing effect was detected in the early-burn treatment (Fig. 18), but it was confined mostly to the first 10 weeks (two sample periods) after burning. After the third sample, production in grazed and ungrazed plots proceeded at a nearly equal rate. A *post hoc* comparison indicated that the differences during the first two periods were not significant. However, caged plot analysis showed biomass loss to herbivores.

Caged clip plots indicated that herbivores removed approximately 0.077kg m^{-2} and 0.064kg m^{-2} from early-burn plots during the first and second sampling intervals. Estimates of forage removed during the third and fourth intervals were obvious anomalies (-0.023kg m^{-2} and -0.012kg m^{-2}). The third and fourth estimates were not considered in the ANPP calculation because they were negative, which was probably a sampling artifact, and because production trends showed little difference between grazed and ungrazed biomass increments during these intervals (Fig. 18). The negative values are a function cage, grazing, or random effects, and perhaps indicate a range of error for the earlier, positive consumption estimates.

A grazing effect was most pronounced in the late-burn treatment for about 15 weeks (3 sample periods) after burning in mid-May (Fig. 18). *Post hoc* comparisons showed a significant difference in late-burn live weight and a near significant difference in total weight (Bonferroni $p \leq .033$). Grazing was apparent on late-burn plots at least five weeks longer than on early-burn plots; late-burn

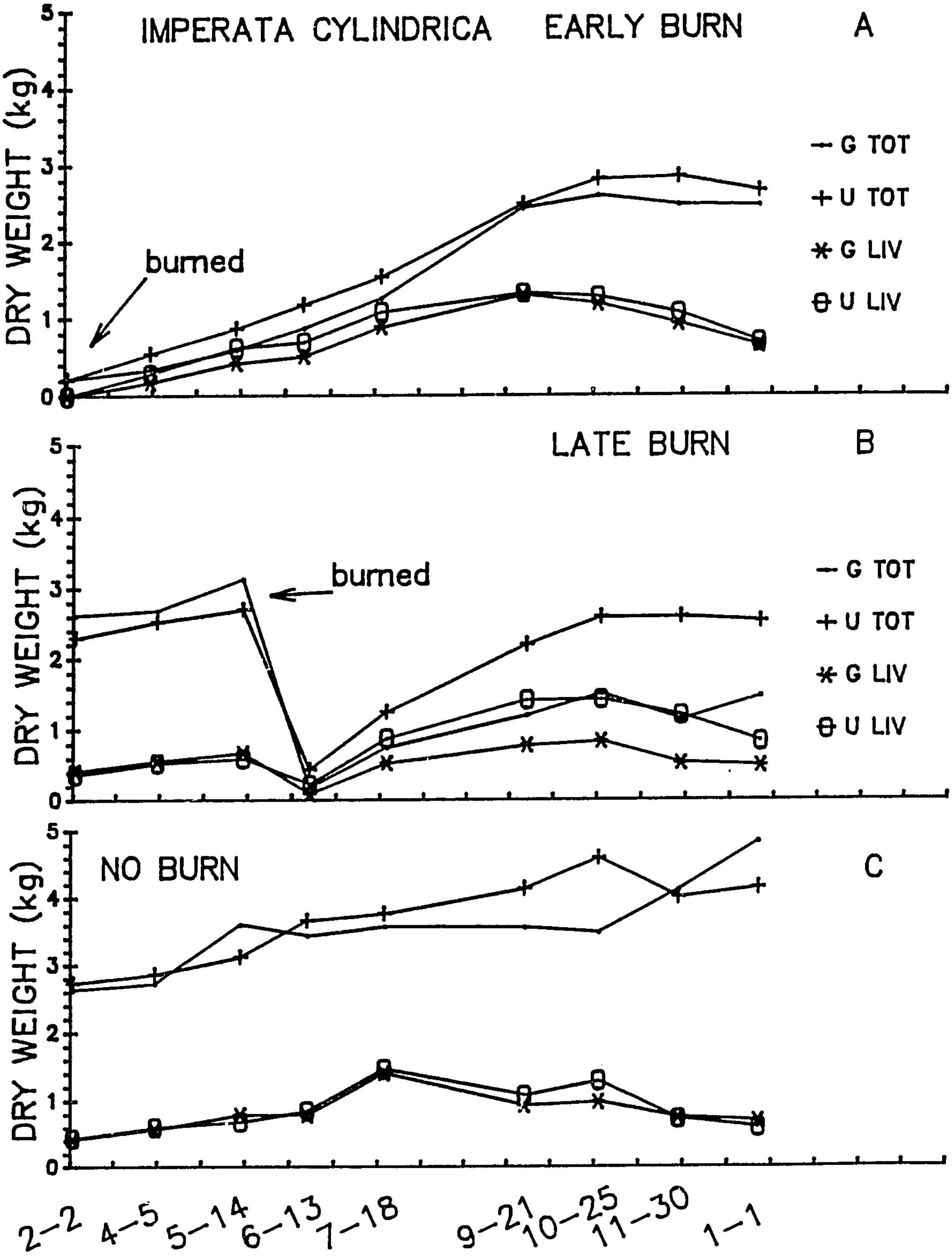

Fig. 18. Time series estimates of *Imperata cylindrica* total biomass (live + dead; TOT in figure) and live biomass (LIV) per 2.25 m^2 plot, both grazed and ungrazed (G=grazed, U=Ungrazed), for burning treatments: A) early burn during late January-early February; B) late burn during May; and C) unburned.

plots provided a flush of tender young foliage among the sea of older forage following legal cutting and burning during late January.

The unburned plots showed little or no grazing effect (Fig. 18). The slight difference after July was likely a random effect; nothing appeared to eat or disturb unburned *Imperata cylindrica*. Herbivores were deterred from foraging by the mass of standing dead material left from the previous year; while, green forage on adjacent burned plots was unobstructed and readily available.

Burning Treatments.--burning had a significant effect on total and live weight of *Imperata cylindrica* (Table 5). Differences between burning treatments are clear for total weight (Fig. 19) and live weight (Fig. 20). Orthogonal comparisons indicted that there was a significant difference between early-burn *vs* unburned, but not early *vs* late burns. A late-burn *vs* unburned comparison was not made to maintain orthogonality, but a difference can be inferred.

Peak live biomass did not appear much different between early-burn and unburned plots, but burned biomass peaked about two months later (Fig. 20). Live biomass in the ungrazed late-burn plots peaked at the same time as early-burn biomass, equalled the other treatments despite the 15-week setback from burning.

Above Ground Net Primary Production.--estimates of *Imperata cylindrica* ANPP were made for each burn treatment by subtracting the starting total biomass from the peak total biomass. Peak total biomass was determined as the leveling point of the total weight curve, or inferred from the point at which live weight peaked, if the total weight curve did not level. Live weight peak biomass was estimated as the actual peak biomass, which was easily discernable.

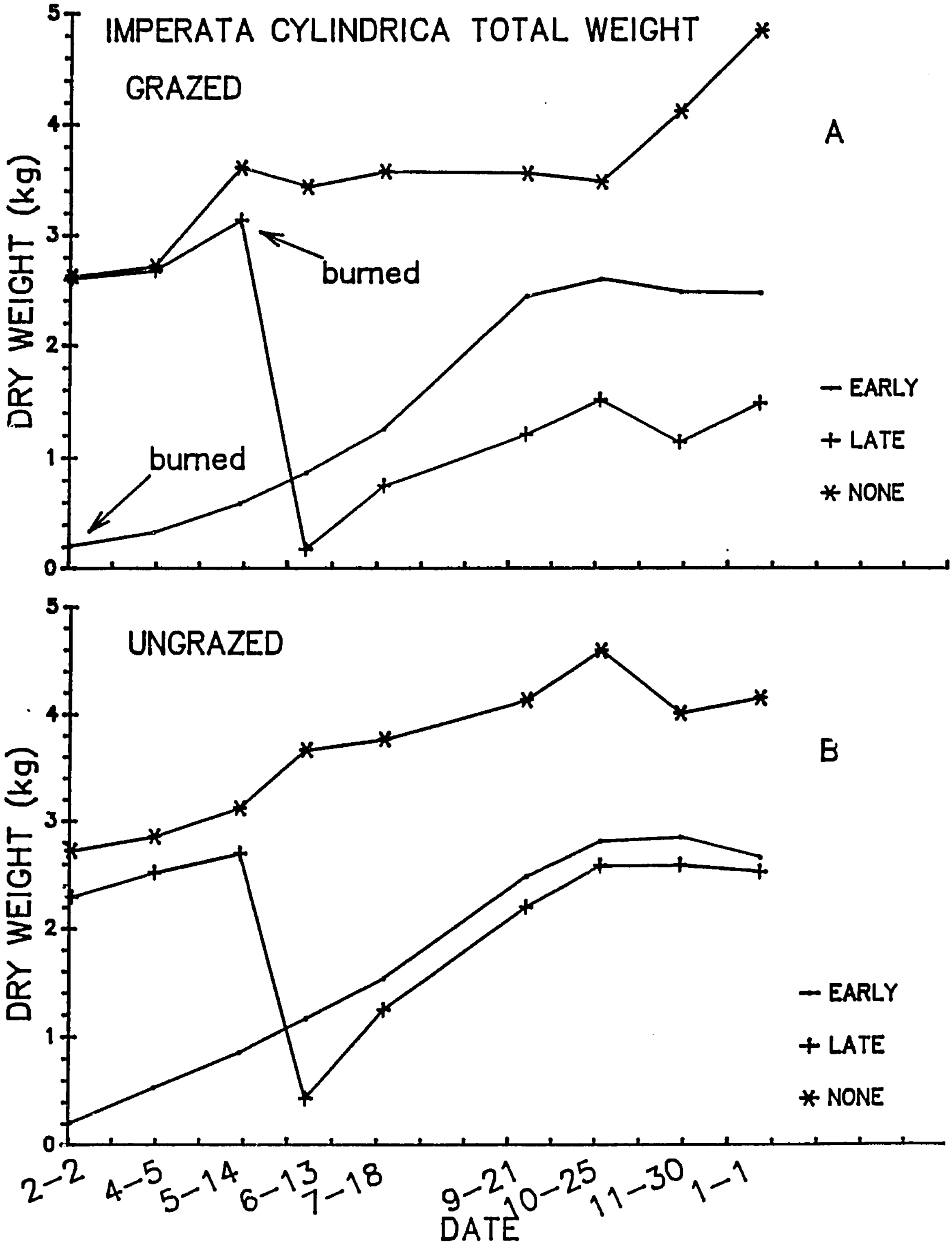

Fig. 19. Total biomass (live + dead) per 2.25 m^2 plot time series for *Imperata cylindrica*, comparing burning treatments. A) grazed treatment plots; B) ungrazed treatment plots.

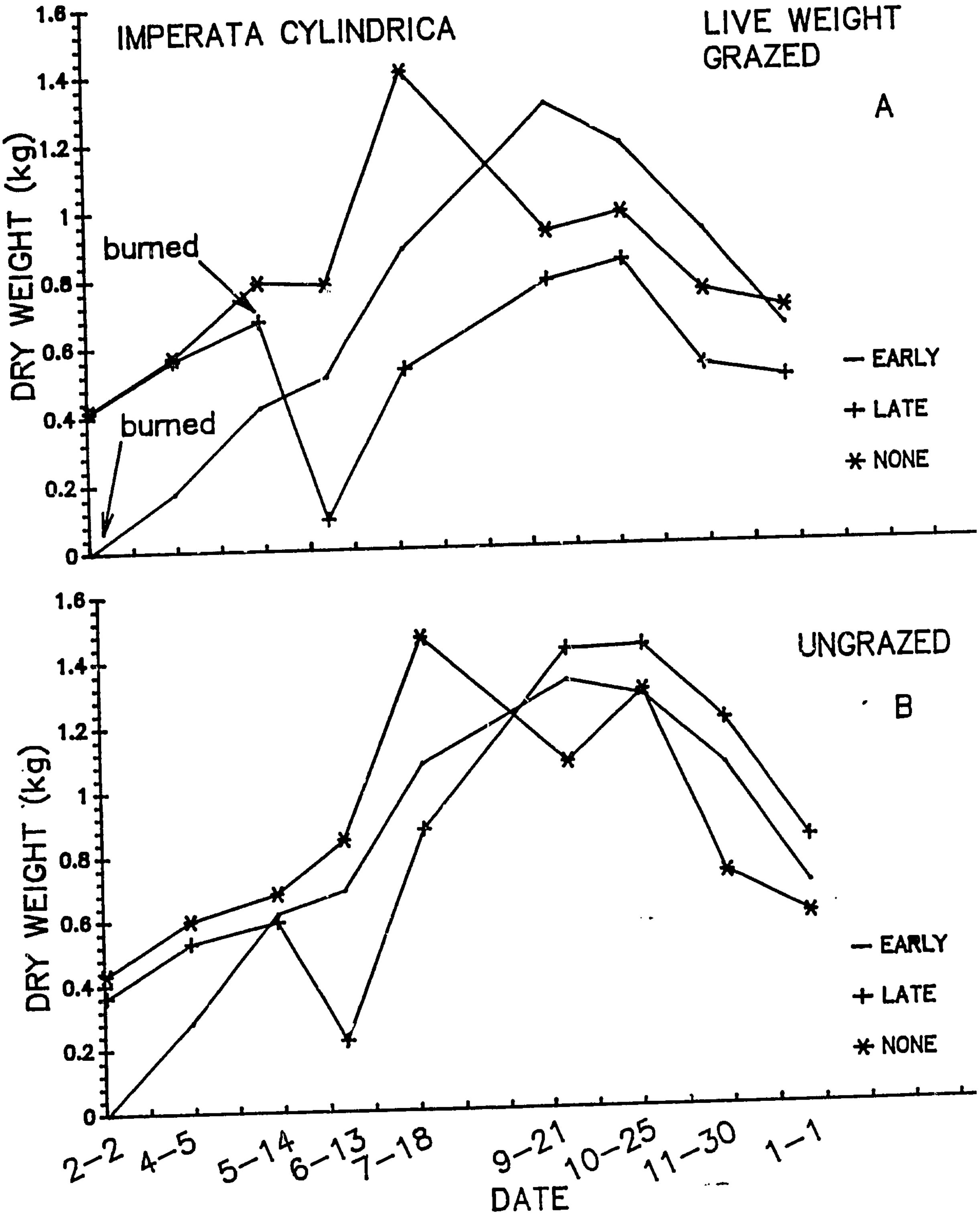

Fig. 20. Live biomass per 2.25 m^2 plot time series for *Imperata cylindrica*, comparing burning treatments. A) grazed treatment plots; B) ungrazed treatment plots.

Grazed and ungrazed ANPP estimates were maintained separately for early and late-burn treatments (Table 6). Grazed and ungrazed plots were pooled to estimate unburned ANPP, as the two estimates were nearly identical and not significantly different.

In all treatments, live weight estimates of production are less than total weight estimates, indicating the transfer of live material into standing dead during the sampling interim. This effect was not observed with the unburned plots. Total weight appears to be the more reliable estimator of ANPP than live weight.

For ungrazed production, early burning production was highest, followed by late-burn and unburned production. Caged plot analysis showed herbivore consumption to be about 12% of the standing biomass.

Narenga porphorycoma (Mixed Tall) Grassland

Ten samples of all the treatment plots were taken from February 1986 through February 1987. One replicate of the unburned treatment and the grazed early-burn plots was burned by wildfire during January 1987, so that regression estimates based on earlier data from those plots were used to estimate biomass for the final, tenth sample. Late-burn plots were sampled through April 1987 to estimate a full year's production from time of burning in early May 1986. These data were not included in the ANOVA, however, to allow for equal sample sizes.

Analysis of variance was done on the total dry weight and the live dry weight (Table 7). Residuals appeared normal in probability plots and tested normal with the Kolmogorov-Smirnov test. Raw residuals and standardized residuals plotted against estimated cell means did not show evidence of heteroscedasticity.

Table 6. *Imperata cylindrica* aerial net primary productivity estimates (kg dry weight m^{-2}) for grazed, ungrazed, and pooled grazing treatments by early-burn, late-burn, and no-burn treatments. Early-burn grazed ANPP estimates include estimated 0.141 kg removed by herbivores. TDW=total dry weight; LDW=live dry weight. * indicates best estimate of production.

	Grazing Treatments					
	Grazed		Ungrazed		Pooled	
Burning Treatments	TDW*	LDW	TDW*	LDW	TDW*	LDW
Early-burn	1.203	0.717	1.172	0.588	....	....
Late-burn	....	....	0.956	0.636	....	....
No-burn	....	....	....	....	0.440	0.448

Table 7. Partial results of analysis of variance for *Narenga porphorycoma* total dry weight and live dry weight biomass estimates in split-block grazing x fire experimental design. (*=$p \leq .1$; **=$p \leq .05$; ***=$p \leq .01$; ****=$p \leq .001$).

TOTAL DRY WEIGHT

Source of Variation	d.f.	SS	MS	F	P
Samples					
Replicates	1	0.638	0.638		
Samples	9	55.026	6.114	4.650	0.016**
Error (S x R)	9	11.834	1.315		
Total	19	67.498			
Treatments					
Grazing	1	0.276	0.276	0.083	0.821 ns
Error (G x R)	1	3.307	3.307		
Burning	2	104.566	52.283	8.263	0.108 ns
Early vs late burn	1	10.720	10.720	1.694	p>0.1 ns
Early vs no burn	1	45.596	45.596	7.205	p>0.1 ns
Error (B x R)	2	12.655	6.328		
Grazing x Burning	2	7.185	3.593	1.762	0.362 ns
Error (G x B x R)	2	4.077	2.039		
Total	10	132.066			

LIVE DRY WEIGHT

Source of Variation	d.f.	SS	MS	F	P
Samples					
Replicates	1	0.316	0.316		
Samples	9	42.130	4.681	15.240	0.000**
Error (S x R)	9	2.764	0.307		
Total	19	45.210			
Treatments					
Grazing	1	0.375	0.375	9.567	0.199 ns
Error (G x R)	1	0.039	0.039		
Burning	2	5.111	2.555	4.656	0.177 ns
Early vs late burn	1	3.544	3.544	6.455	p>0.1 ns
Early vs no burn	1	0.020	0.020	0.036	p>0.1 ns
Error (B x R)	2	1.097	0.549		
Grazing x Burning	2	1.827	0.913	18.368	0.052*
Error (G x B x R)	2	0.099	0.050		
Total	10	8.548			

ANOVA for total weight and live weight both showed a significant effect from sampling period as might be expected (Table 7). However, grazing and burning treatments were not significant for total weight or live weight.

Grazing Treatment.--grazing did not have a significant effect on *Narenga porphorycoma* total weight or live weight (Table 7). The grazing effect appeared greater for live weight, but this was probably an anomaly as indicated by the significant grazing x burning interaction term. Early-burn plots appeared to show a grazing effect during the first ten weeks of sampling (Fig. 21). However, *post hoc* tests of grazed *vs* ungrazed within burn treatment effects showed no significant difference (Bonferroni $p \leq 0.033$) for total weight or live weight.

Caged-plots to estimate consumption and grazed production were discontinued after the second sample. There was little visible evidence of grazing, variability between the paired plots was too great relative to differences in biomass, and the effort required to process the samples large relative to significant information. For example, estimated production for the early-burn treatment during the first interval as measured by the cage-plot technique was -0.121 kg/m^2, compared to 0.054 kg m^{-2} for the uncaged technique, despite an obvious live biomass increase (Fig. 21A).

Herbivores do graze this species after fire induces new growth; particularly well known is the movement of small bands of gaur *(Bos gaurus)* down from the Churia Hills during this time. However,herbivore density is low in these stands, and grazing would have a minor impact on the super-abundant forage biomass available at that time.

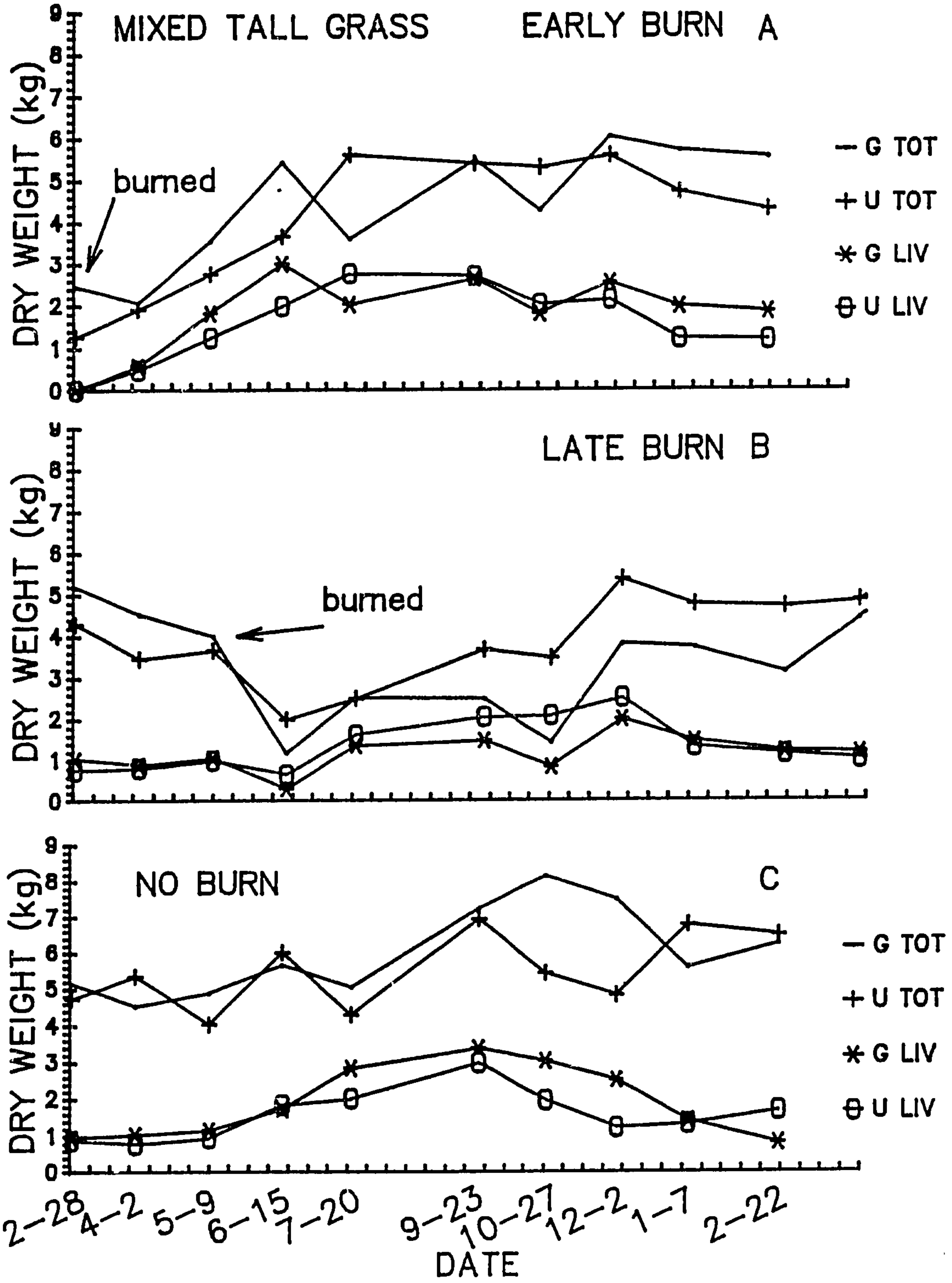

Fig. 21. Time series estimates of *Narenga porphorycoma* total biomass (live + dead; TOT in figure) and live biomass (LIV) per 2.25 m^2 plot, both grazed and ungrazed (G=grazed, U=Ungrazed), for burning treatments: A) early burn during late January–early February; B) late burn during May; and C) unburned.

Late-burn plots showed an apparent grazing effect from 5 to 10 weeks after burning (Fig. 21). *Post hoc* tests, however, showed no significant difference within the treatment. Grazing might be expected at this time when the mass of earlier-burned grasses has become tall and unpalatable. However, herbivore abundance in these grass communities is low, and the small burned patches might not have been easily found or were insufficiently attractive.

Unburned plots showed an apparent reverse grazing effect after the fourth sample on June 15 (Fig. 21). I can only suggest that this is sampling error, as this pattern is opposite that expected for grazing. Very little, or no grazing was observed in these, or any plots; grazing would be expected to be highest in the burned plots where live material was most accessible to herbivores. The significant interaction term in the live weight ANOVA is a function of this reversed-grazing effect.

I pooled the grazed and ungrazed data for each burn treatment to better estimate ANPP (Fig. 22). The apparent grazing effects were not significant, and a constant difference in biomass was not evident in the curves for later samples, as with the *Imperata cylindrica* stand. *Narenga porphorycoma* biomass production peaked on early- and unburned plots during late September and early October. Late-burn biomass apparently peaked in early December; but, the trend established before and after the peak suggests declining production from late September, which is probably correct. The high biomass value for December is probably sampling error.

Burning Treatments.--burning did not have significant effects on *Narenga porphorycoma* total weight and live weight (Table 7). However, grazed and ungrazed samples pooled for each burning treatment show very clearly a lower biomass for the late burn (Fig. 23A). The increase in total biomass for the last

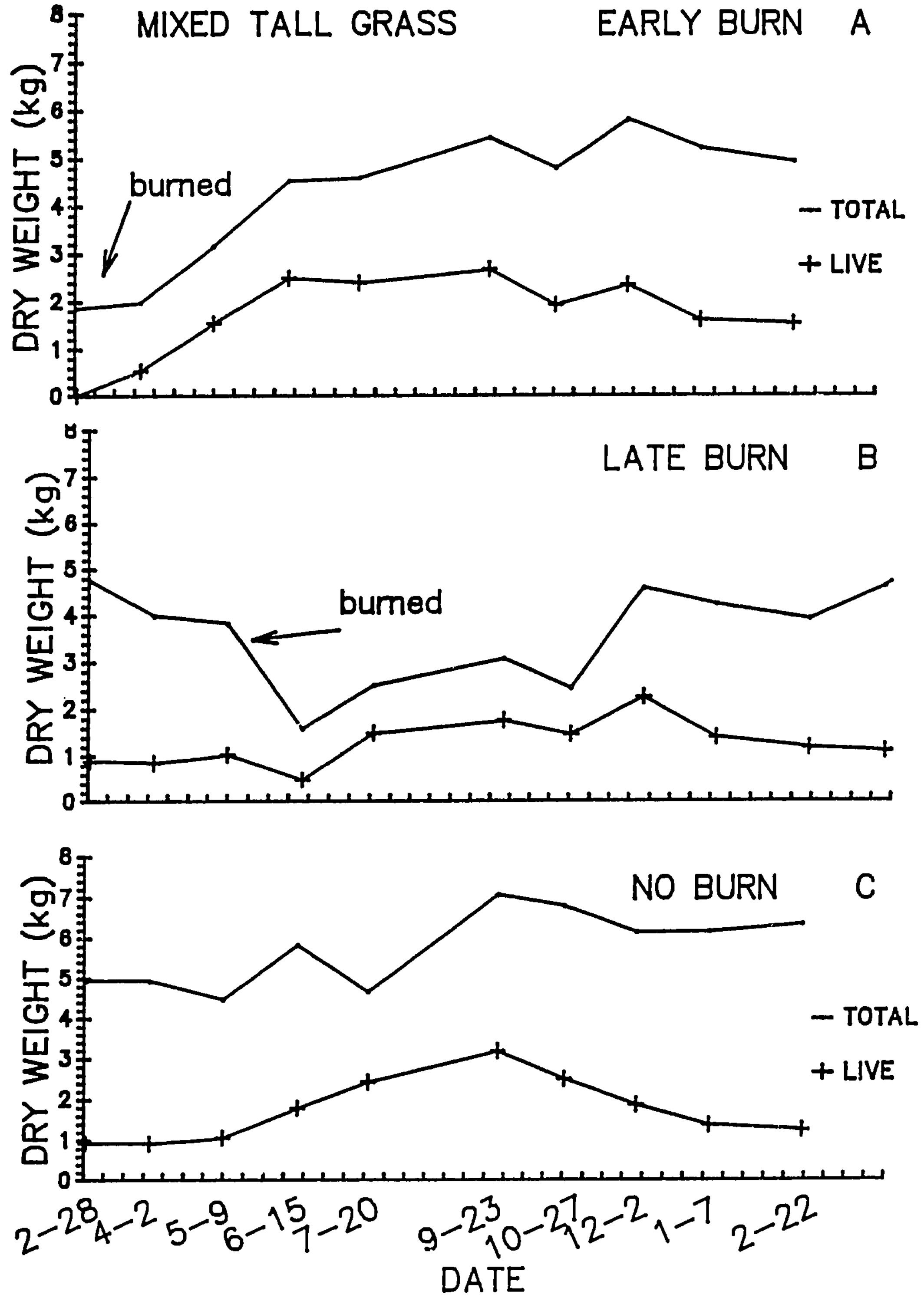

Fig. 22. Pooled grazed and ungrazed time series of *Narenga porphorycoma* total biomass (live + dead; TOT in figure) and live biomass (LIV) per 2.25 m^2 plot by burn treatment. A) early burn during late January-early February; B) late burn during May; and C) unburned.

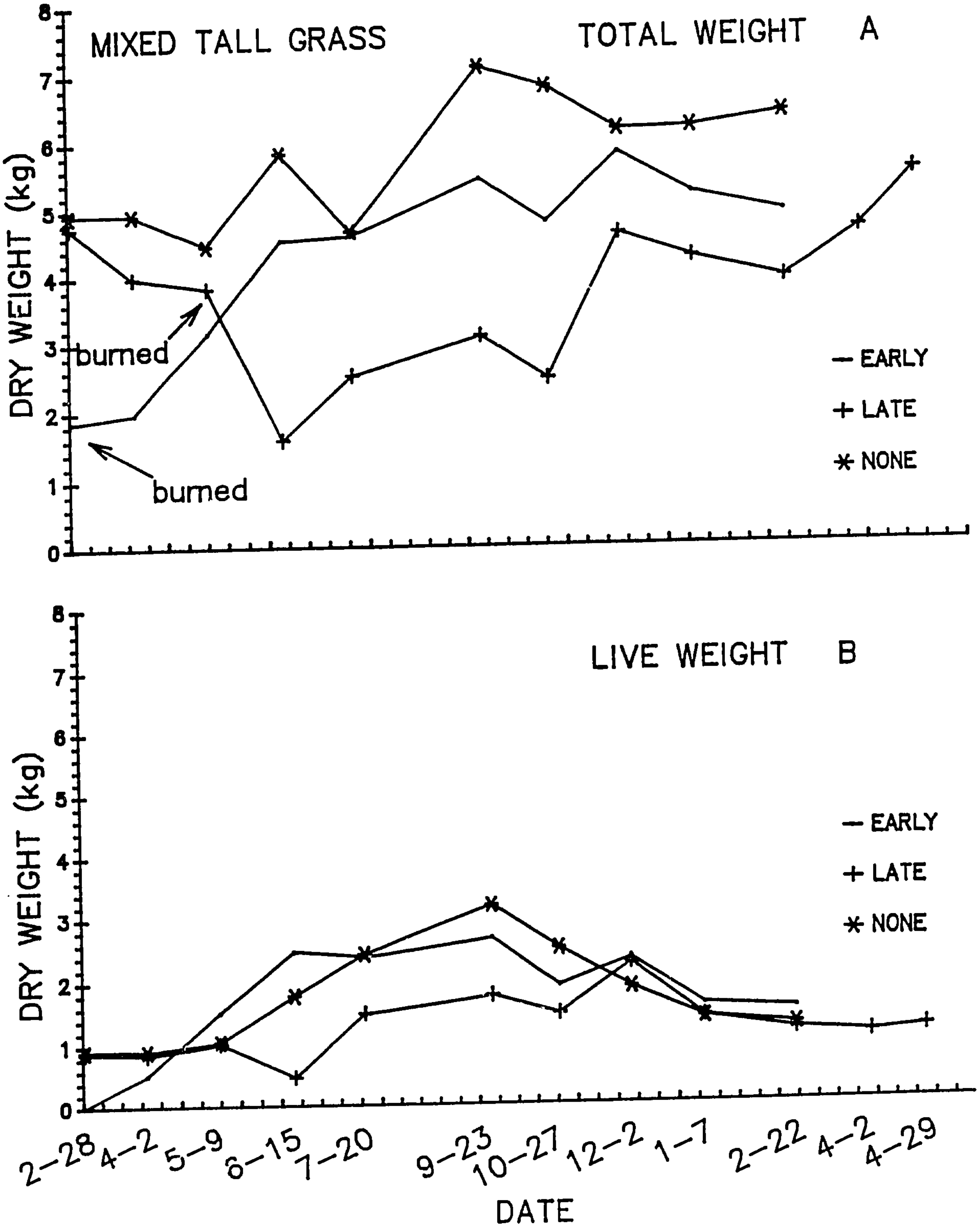

Fig. 23. Total and live biomass per 2.25 m^2 plot time series for *Narenga porphorycoma*, comparing burning treatments. Grazing treatments pooled.

two samples is probably an artifact due to variability in dead biomass; live weight does not show the same trend (Fig. 23B). Early and unburned treatments are not very different in live biomass after 10 weeks of growth following fire in the early-burn plots.

Aerial Net Primary Production.--early burning resulted in the greatest *Narenga porphorycoma* production, followed by late-burn and unburned production. The early-burn treatment produced 30-130% more biomass than unburned and late-burn plots (Table 8). As with *Imperata cylindrica,* the early-burn total weight estimate was higher than the live weight; positive increments in dead material weight indicated that live matter was being lost during the sampling interval so that total weight is the better estimator of ANPP.

Late-burn estimates did not show the expected higher value for total weight than for live weight, probably because of sampling error and heterogeneity in the treatment plots with respect to biomass distribution. Unburned total and live weight ANPP estimates were not greatly different, indicating little loss of live material to the dead compartment during the sampling interval.

Saccharum spontaneum Grassland

This was a difficult site. Site selection was feasible only in November, but by that time elephant handlers had cut fodder from most of the productive and accessible stands. However, I was able to locate an uncut site in an acceptable mid-range of productivity.

Shortly after fire lanes were cut, elephant handlers cut some grass from the plots. This intrusion was not too serious, as the cut patches were legitimate defoliation of unfenced plots. However, handlers later cut inside the exclosure. More intrusion occurred during the dry season from March through May when

Table 8. *Narenga porphorycoma* aerial net primary productivity estimates (kg dry weight m^{-2}) for pooled grazing treatments by early-burn, late-burn, and no-burn treatments. TDW=total dry weight; LDW=live dry weight. * indicates best estimate of production.

	Grazing Treatments					
	Grazed		Ungrazed		Pooled	
Burning Treatments	TDW*	LDW	TDW*	LDW	TDW*	LDW
Early-burn	....	....	....	....	1.590	1.183
Late-burn	....	....	....	....	0.668	0.780
No-burn	....	....	....	....	0.952	1.009

villagers sneaked into the Park and cut grass from plots inside and outside the exclosure. Illegal cutting was not a problem after May for the remainder of the year.

Avoiding heavily disturbed areas in the treatment plots, I continued sampling through January 1987 to salvage some information about fire effects on production. An attempt at a tenth cutting in February to sample through a complete year was aborted upon discovery that villagers had cut much of the new growth.

Analysis of variance of total weight showed no significant effects from sampling period, grazing, burning, or grazing x burning interaction (Table 9). Analysis of residuals did not indicate significant deviation from normality. Analysis of live weight variance, however, indicated significant effects for sample, burning, and grazing x burning interaction.

Patterns of biomass accumulation were similar for total weight and live weight, because most of the current years production goes into stems and little into leaves (Fig. 24). Some of the variance in total weight can be accounted for by dead material from the previous year. Most of this dead material resulted from defoliation by elephant handlers and villagers cutting fodder.

Grazing Treatments.--grazing did not have a significant effect on *Saccharum spontaneum* live weight, but a significant grazing x burning interaction suggested significant effects within individual treatments. *Post hoc* tests showed a significant grazing effect only within the early-burn treatment (Bonferroni $p \leq .033$).

Table 9. Partial results of analysis of variance for *Saccharum spontaneum* total dry weight and live dry weight biomass estimates in split-block grazing x fire experimental design. (*=p≤.1; **=p≤.05; ***=p≤.01; ****=p≤.001).

TOTAL DRY WEIGHT

Source of Variation	d.f.	SS	MS	F	P
Samples					
Replicates	1	0.030	0.030		
Samples	8	44.847	5.606	1.645	0.249 ns
Error (S x R)	8	27.261	3.408		
Total	17	72.138			
Treatments					
Grazing	1	12.069	12.069	6.450	0.239 ns
Error (G x R)	1	1.871	1.871		
Burning	2	56.587	28.293	4.229	0.191 ns
Early vs late burn	1	11.967	11.967	1.789	p>0.1 ns
Early vs no burn	1	16.445	16.445	2.458	p>0.1 ns
Error (B x R)	2	13.381	6.690		
Grazing x Burning	2	7.238	3.619	6.741	0.129 ns
Error (G x B x R)	2	1.074	0.537		
Total	10	92.219			

LIVE DRY WEIGHT

Source of Variation	d.f.	SS	MS	F	P
Samples					
Replicates	1	0.004	0.004		
Samples	8	52.949	6.619	7.707	0.005***
Error (S x R)	8	6.870	0.859		
Total	17	59.823			
Treatments					
Grazing	1	3.058	3.058	3.491	0.313 ns
Error (G x R)	1	0.876	0.876		
Burning	2	24.967	12.484	14.752	0.063*
Early vs late burn	1	4.776	4.776	5.645	p>0.1 ns
Early vs no burn	1	7.834	7.834	9.260	p<0.1*
Error (B x R)	2	1.692	0.846		
Grazing x Burning	2	2.871	1.435	16.913	0.056*
Error (G x B x R)	2	0.170	0.085		
Total	10	33.634			

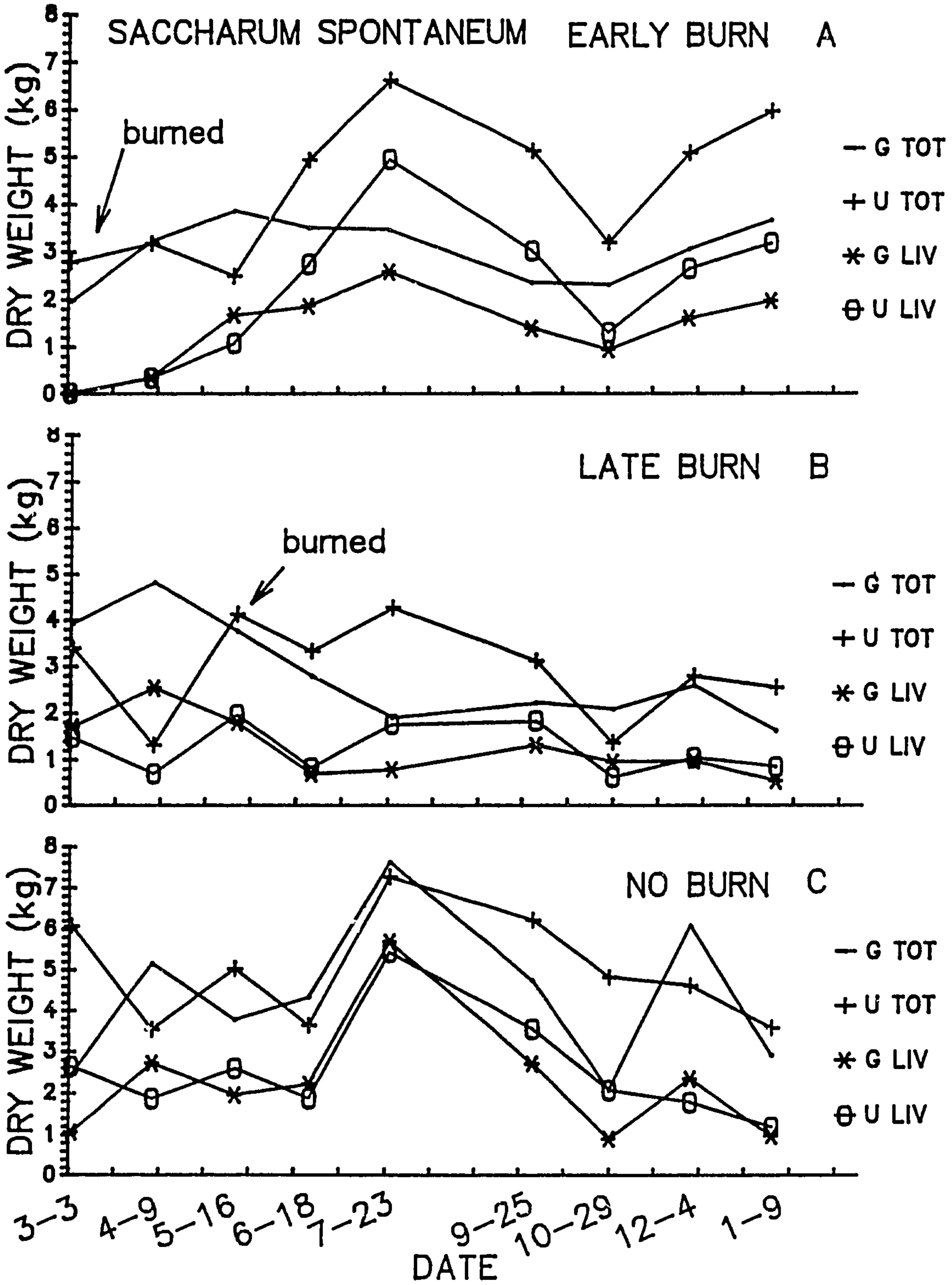

Fig. 24. Time series estimates of *Saccharum spontaneum* total biomass (live + dead; TOT in figure) and live biomass (LIV) per 2.25 m^2 plot, both grazed and ungrazed (G=grazed, U=Ungrazed), for burning treatments: A) early burn during early February; B) late burn during May; and C) unburned.

However, intrusion of villagers and elephant fodder cutters early in the growing season makes interpretation of grazing effects problematic and difficult to make with confidence. Therefore, grazed and ungrazed production were pooled for further analysis (Fig. 25).

Burning Treatments.--burning treatments were not significantly different with respect to total weight, despite apparent differences (Fig. 26A). Live weight showed trends nearly identical to total weight, but the differences in live weight between burn treatments were significant (Fig 26B). Orthogonal comparisons between treatments indicated a significant difference between live weights of the early and unburned treatments, but not between early and late burns. A difference between late and unburned treatments is inferred from their position relative to early burn.

Biomass on early-burned plots peaked in late July, and then showed a steady decline. Late-burn biomass declined steadily after burning in mid-May. Plants had already begun to produce new shoots at the time of burning and had a heavy investment in new shoots.

Biomass on unburned plots appeared to increase slowly prior to June, then rapidly reached a peak in late-July (Fig. 26). Much of the pre-June production was probably removed by grass cutters, and greater production might have been measured during this time if not for defoliation. The relatively low June value is probably sampling variation, but the jump in mid-July corresponds to the onset of the monsoon rains.

Aerial Net Primary Productivity.--the relationship between total weight and live weight is reversed from other sites; live weight estimates are higher than the total weight estimates (Table 10. I think that the live weight estimates are more accurate because most of the production goes into stem

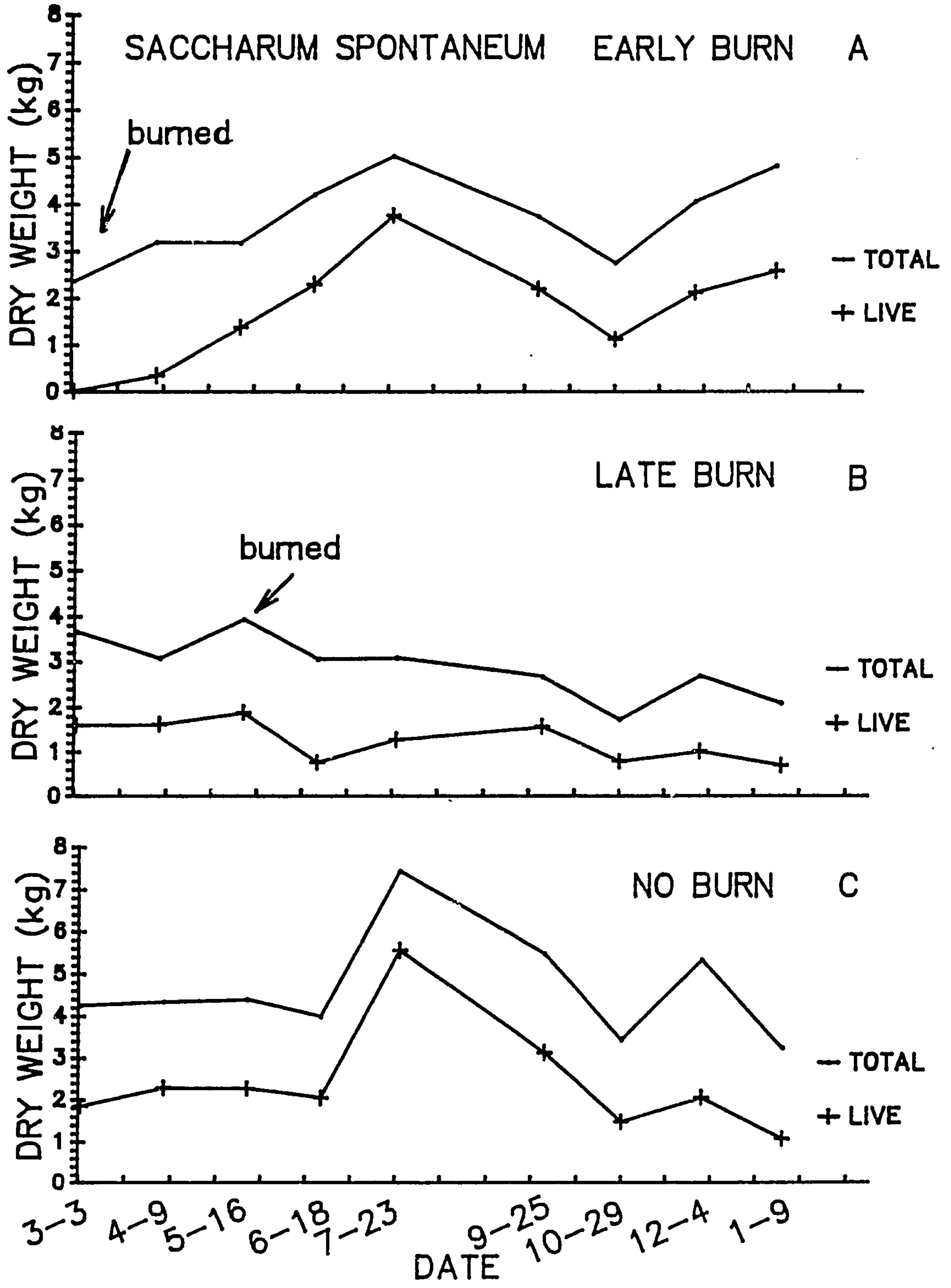

Fig. 25. Pooled grazed and ungrazed time series of *Saccharum spontaneum* total biomass (live + dead; TOT in figure) and live biomass (LIV) per 2.25 m^2 plot by burn treatment. A) early burn during late January-early February; B) late burn during May; and C) unburned.

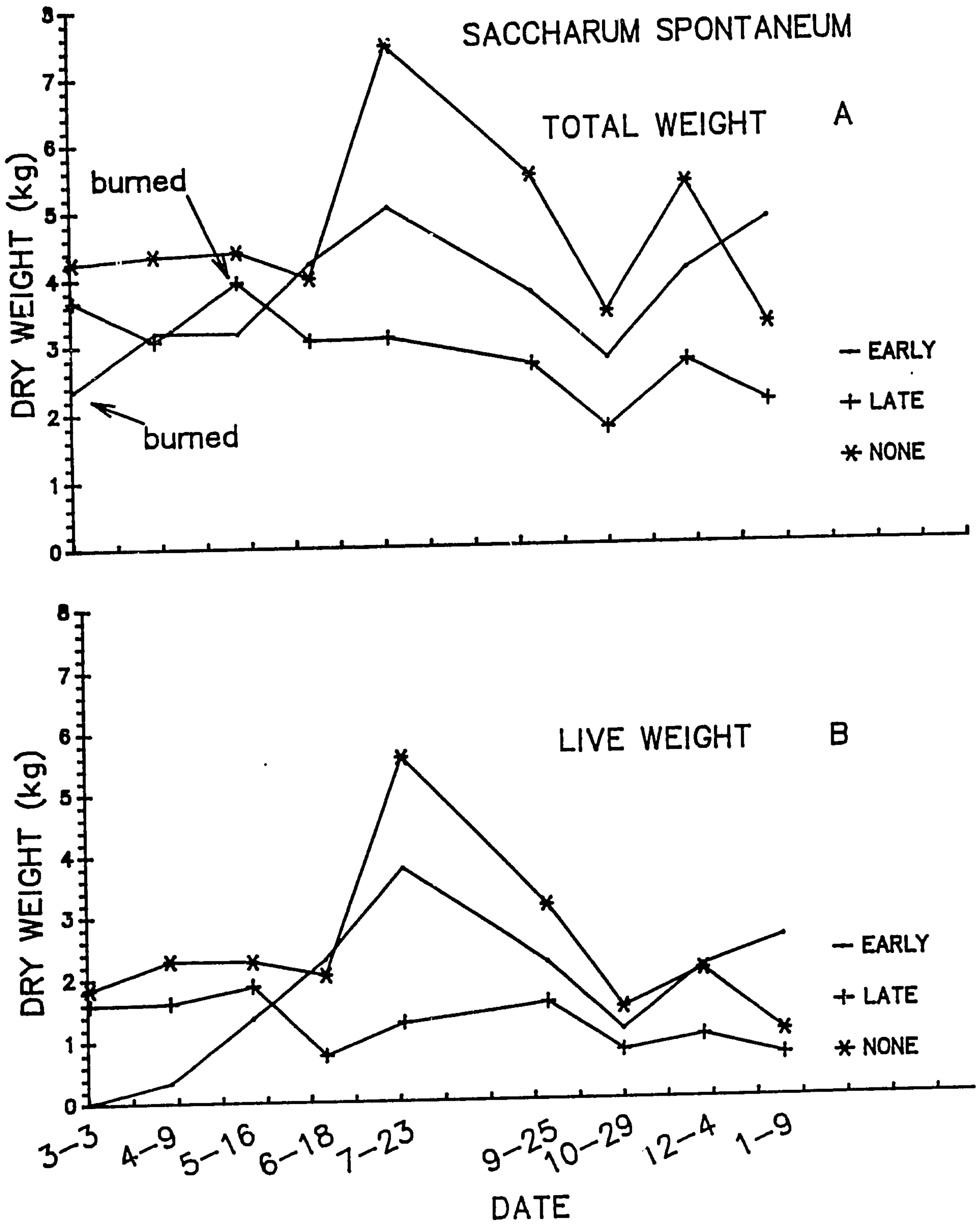

Fig. 26. Total and live biomass per 2.25 m^2 plot time series for *Saccharum spontaneum*, comparing burning treatments. Grazing treatments pooled.

Table 10. *Saccharum spontaneum* aerial net primary productivity estimates (kg dry weight m^{-2}) for grazed, ungrazed, and pooled grazing treatments by early-burn, late-burn, and no-burn treatments. TDW=total dry weight; LDW=live dry weight. * indicates best estimate of production.

	Grazing Treatments					
	Grazed		Ungrazed		Pooled	
Burning Treatments	TDW	LDW*	TDW	LDW*	TDW	LDW*
Early-burn	0.671	1.144	1.706	2.192	1.188	1.668
Late-burn	....	....	....	....	....	0.361
No-burn	....	....	....	....	1.420	1.651

material and very little into leafy material that is likely to age during the sampling interval. Total weight estimates are probably lower because of a higher variability in occurrence of dead stems from the previous year in a plot, and some random sampling error.

ANPP base on live weight was about equal for early and unburned plots. Biomass on late-burn plots decreased after burning, so there was no net production. These estimates must be viewed with caution, however, because human disturbance eliminated experimental control of defoliation for estimating true ANPP.

Environmental Determinants of ANPP

Soil Moisture.--the *Imperata cylindrica* and Mixed Tall Grass sites had similar patterns of soil moisture throughout the year (Fig. 27). Soil moisture was about 25-30% during January, the beginning of the growing season. Soils dried somewhat during the hot spring to just below 20% moisture.

Soil moisture rose during May with the pre-monsoon showers, continuing to rise through June as monsoon rains began. A nearly constant 30% moisture was maintained through the monsoon and fall. The cyclic change exhibited by all the samples is really inexplicable; perhaps, it coincided with periods of relative dryness, or it could have been some unknown systematic error.

The young alluvial *Saccharum spontaneum* soils showed a quite different pattern than the older upland *Imperata cylindrica* and mixed tall grass soils, which are relatively similar in development. Soil moisture in the sandy *Saccharum spontaneum* soil during January was about 10%. As with the other sites, soil moisture dropped during the hot spring, but much lower to about 5%. However, soil moisture quickly rose through late April and early June to 25-30%, reaching this

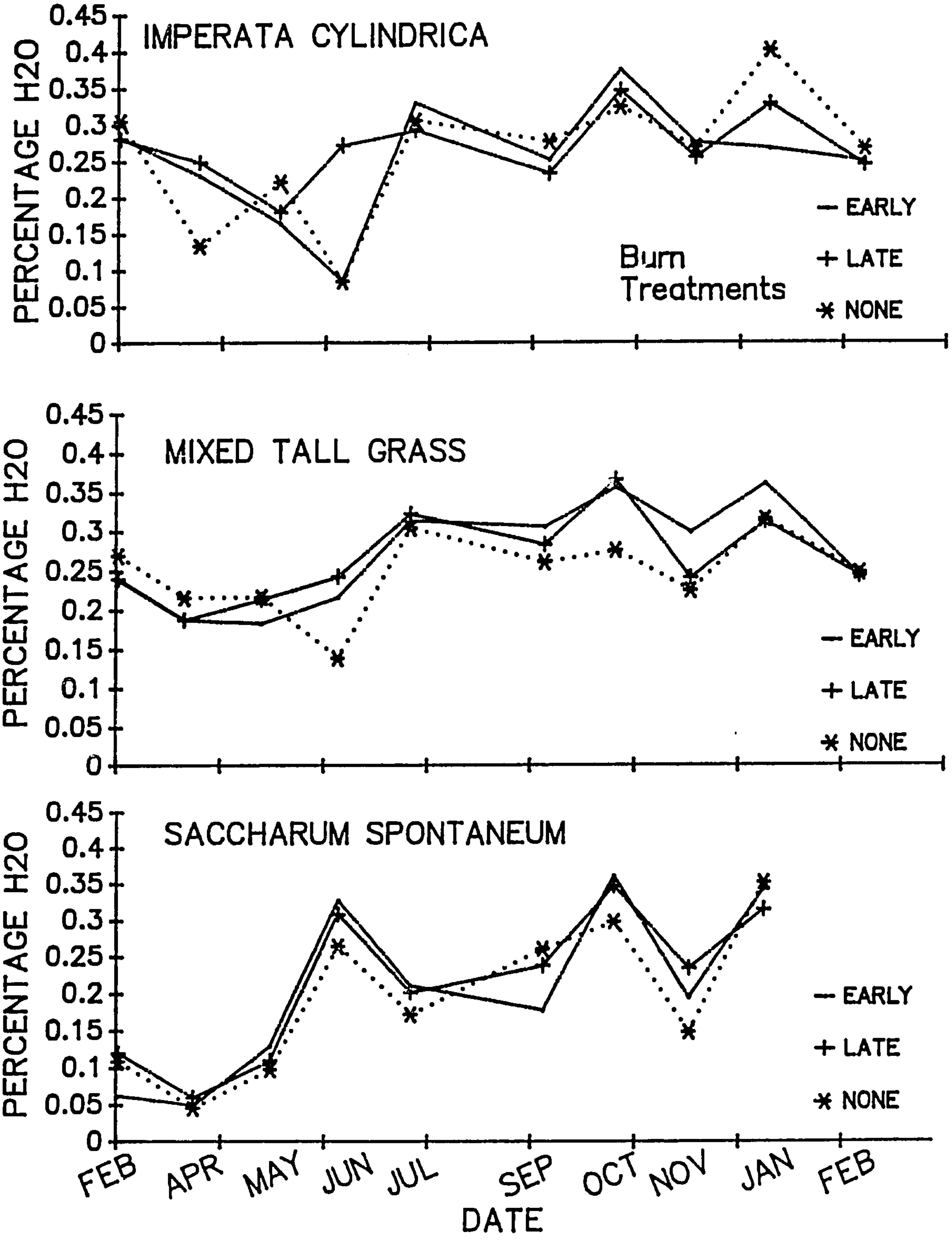

Fig. 27. Soil moisture percentage by burn treatment for three experimental sites. Grazing treatments pooled.

amount before the upland sites. Soils appeared to dry slightly during the remainder of the monsoon, and later fluctuate during the fall. The fluctuations were nearly as regular as with upland sites; the causes were probably similar.

Analysis of variance revealed a significant ($p \leq .05$) site difference. Orthogonal comparisons demonstrated a significant difference ($p = .01$) between the *Saccharum spontaneum* site and the grouped *Imperata cylindrica* and Mixed Tall Grass sites, but not between the *Imperata cylindrica* and Mixed Tall Grass sites. There was no significant burning treatment effect.

Soil Temperature.--as with soil moisture, *Imperata cylindrica* and Mixed Tall Grass sites had similar patterns of soil surface temperature (Fig. 28). Early burning on both sites elevated surface temperatures 6-8°C during spring into June. The effect was more pronounced on the *Imperata cylindrica* site where the low canopy less effectively shaded the ground than in Mixed Tall Grass sites.

Late burning had similar effects at the *Imperata cylindrica* and Mixed Tall Grass sites. Temperature initially rose less than 3°C on the mixed tall grass plots, but jumped over 8°C from the unburned condition on the *Imperata cylindrica* plots, and remained consistently higher than mixed tall grass through the summer. This was the result of high insolation caused by grazers cropping the swards low and reducing shade on the ground surface.

Surface temperature of sandy-soil *Saccharum spontaneum* plots followed an apparently different pattern than upland sites. Post-burn February temperatures for all burn treatments were about 27°C; this was higher than unburned plots, but the same as early-burn plots, on the other two sites. Temperature peaked near 38°C during the hot spring month of April, then dropped to a summer level of about 29°C during the summer.

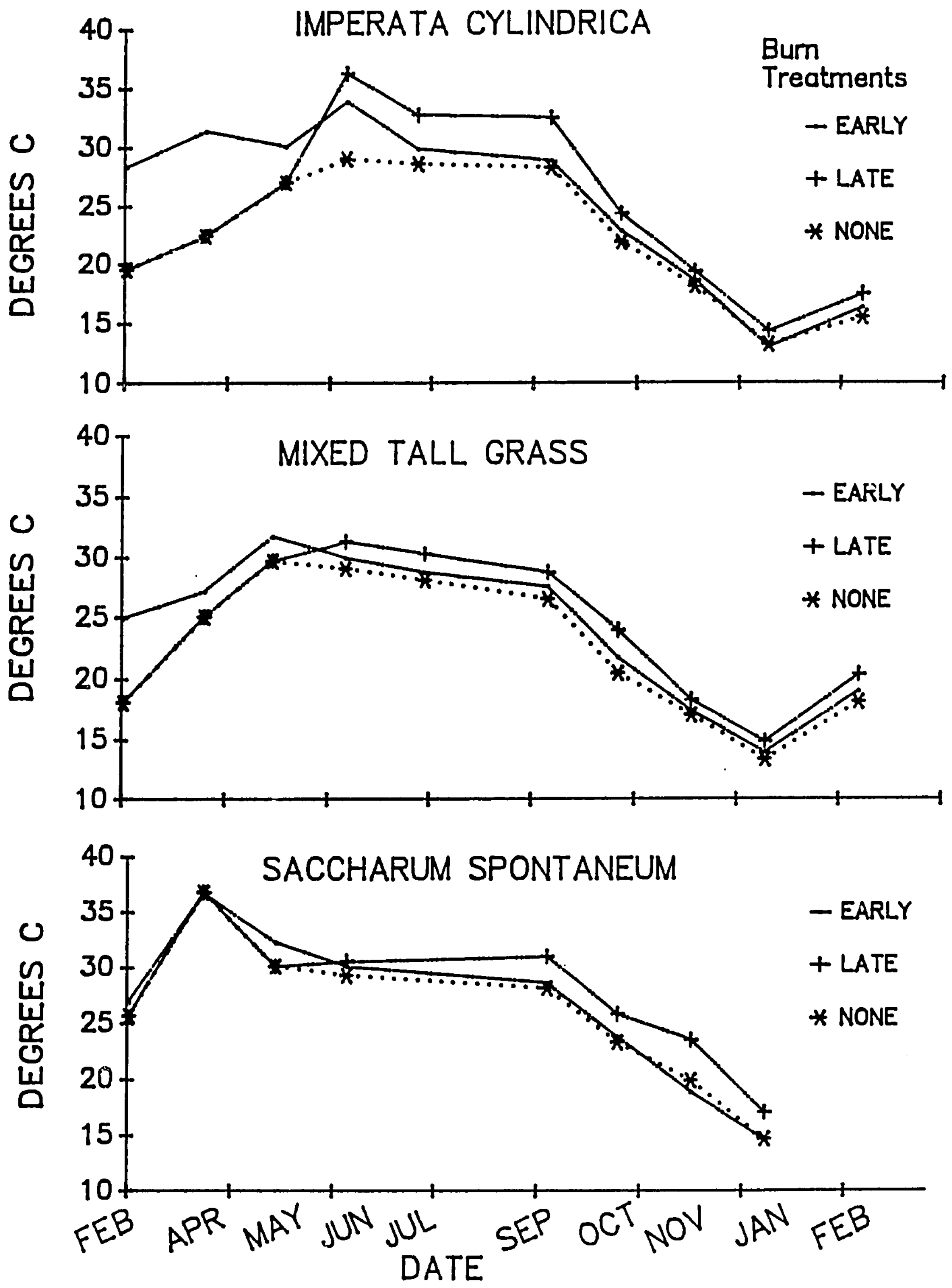

Fig. 28. Soil surface temperature by burn treatment for three experimental sites. Grazing treatments pooled.

Summer soil temperatures were about 29°C on all three sites during the summer. Soil surfaces began to cool rapidly after September, and earlier differences from burning treatments became less. Temperature began to rise again in January where measured.

GRAZING LAWN ANPP

Composition

Chrysopogon asciculatus dominated the grazed pasture with nearly 37% ground cover and 45% of the vegetative cover (Table 11). Nearly equal subdominants were *Cynodon dactylon* and short-cropped *Imperata cylindrica* with about 19% cover. These three grasses constituted over 92% of the vegetative cover. *Hemarthria compressa* was not observed in the samples, but is known to be minor grass component of the lawn. The annual legume *Cassia tora* also was patchily abundant throughout the pasture during monsoon.

Imperata cylindrica grew to about .5 m height and dominated the ungrazed pasture within one year. *Saccharum spontaneum* plants, released from grazing inside the exclosure, rapidly grew to 3-4 m height within a year. Fifty one clumps of *Saccharum spontaneum* developed in the 485 m^2 fenced area, a density of 0.11 clumps m^{-1}.

ANPP on Grazed and Ungrazed Pasture

Primary Production.--production on the grazed pasture was about half that of the ungrazed exclosure (Fig. 29). Total production on the ungrazed site was estimated at 1410 gm m^{-2} (after subtracting initial from final biomass); approximately 872 gm m^{-2} was produced on the grazed pasture. Growth peaked by early September on the grazed plots. Production continued at least another month

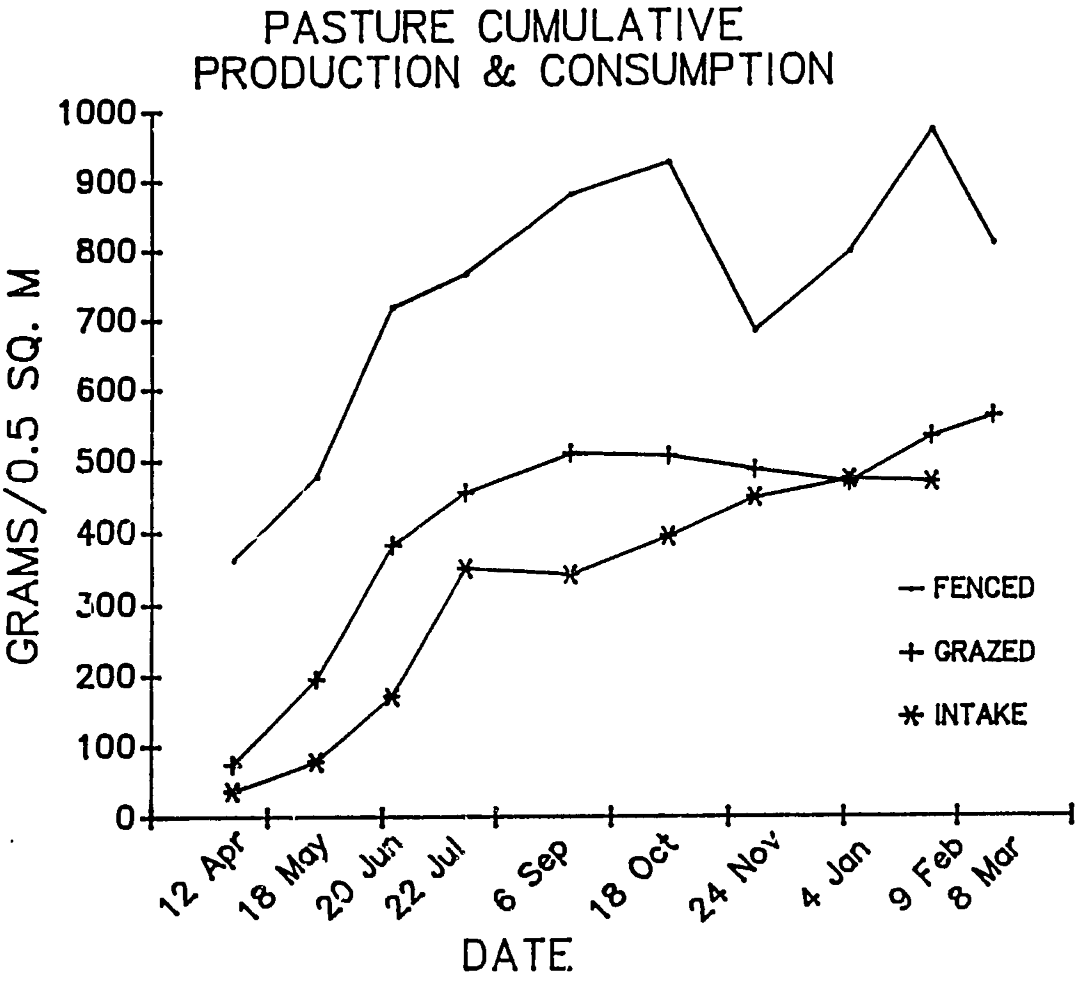

Fig. 29. Cumulative biomass production and forage intake by domestic livestock on the Hattisar pasture, Sauraha, Chitwan, during 1986 and 1987. Production was estimated both inside and outside an exclosure.

Table 11. Composition of Sauraha Hattisar pasture as determined by point-frame sampling on 11 transects, each with 10 stations, April 1987.

Species	Total Points	Percent Total	Percent Composition
Monocots			
Chrysopogon asciculatus	205	36.9	44.9
Cynodon dactylon	109	19.6	23.9
Imperata cylindrica	105	18.9	23.0
sedge spp.	8	1.4	1.8
Paspalum sp.	4	0.7	0.9
Saccharum spontaneum	3	0.5	0.7
Vetiveria zyzanioides	3	0.5	0.7
Dicots			
Trifolium sp.	17	3.1	3.7
Lippia nodiflora	3	0.5	0.7
Dead biomass	78	14.1	..
Bare ground	20	3.6	..
Total	555		

on the ungrazed plots; this was partly a result of removing grazing and changed species composition.

After a fall dormant season, production resumed during January on grazed plots (Fig. 29). The rapid drop shown for ungrazed production during the fall was the result of villagers entering the exclosure during the night and cutting grass for a festival. The exclosure was the only place outside the Park where long *Imperata cylindrica* was available; also, the danger at night from large mammals was much less on the pasture than in the Park's jungle.

Studies in the Park of similar, undisturbed *Imperata cylindrica* stands revealed some growth during January, with the highest rate during late June and early July (Fig. 18). In contrast, the peak rate of grazed pasture growth occurred during late May and early June. Subsequent phenology on the ungrazed pasture would likely have followed the inside-Park pattern, if the experiment had continued.

Primary Consumption.--livestock consumed all of the annual production on the grazed pasture (Fig. 29). Consumption followed production closely during the peak early-summer growth season. Intake then appeared to fall off during mid-summer, but resumed during the fall at a lower rate than early summer. By the beginning of the new growing season in January, consumption had matched production.

An average of 198 head of livestock (± 67; alpha=.05) were found grazing the general pasture area during a sample day (Table 12). The area of the pasture was about 8 ha. About 70% of the stock were cattle; 12% were water buffalo. Stock were not kept in the pasture all day, but were move along a daily grazing circuit. Counts could not always be made at the exact same time, and livestock movements

Table 12. Livestock counts on the Sauraha Hattisar (elephant camp) pasture. Confidence interval for total mean is at p=.05.

DATE	BA	BSA	BC	CA	CSA	CC	GOATS	SHEEP	TOTAL
02-May-86	..	..	..	105	..	..	..	..	105
14-May-86	..	..	..	145	..	..	..	..	145
06-Jun-86	5	..	..	108	..	12	..	..	125
03-Jul-86	9	3	3	48	24	13	8	30	138
25-Jul-86	8	1	..	382	..	19	..	..	410
02-Aug-86	109	..	..	155	86	..	..	..	350
13-Aug-86	..	3	..	15	..	..	..	..	18
26-Aug-86	22	..	..	58	..	..	..	..	80
07-Sep-86	3	2	..	150	29	8	..	..	192
29-Sep-86	..	..	..	112	..	..	..	..	112
12-Nov-86	53	32	..	111	34	..	..	..	230
24-Nov-86	50	7	9	136	25	..	..	..	227
16-Jan-87	15	8	..	155	65	32	23	..	298
11-Mar-87	58	16	..	246	14	6	..	..	340
Means	24	5	1	138	20	6	2	2	198 ± 67

BA - Adult buffalo; BSA - Subadult buffalo; BC - Buffalo calf
CA - Adult cow/bullock; CSA - Subadult cow/bullock; CC - Calf

were not entirely regular. This accounts for the variation in stock counts throughout the year.

Effects of Defoliation on Pasture Production

Defoliation had a definite negative effect on production; grasses did not overcompensate as hypothesized in grazing optimization theory (Fig. 30). Analysis of variance indicated a significant treatment effect ($p=.001$). Orthogonal comparisons of adjacent treatments revealed a significant difference only between 45-day and 90-day defoliation treatments. *Post hoc* comparison of the first 3 treatments against the fourth showed a significant difference (Bonferroni $p<.025$); the first 2 treatments together were not different from the third.

Production on control and 90-day defoliation and control plots should actually be slightly higher than pictured in Fig 30. Some cows got into the exclosure one morning during September and removed some biomass from these plots, and villagers later removed some biomass under cover of night. Tests showed no significant difference between 90-day defoliation and control plots.

The level of grazing defoliation on the pasture was greater than the most severe defoliation intensity in the experiment. Grazed pasture production was 61% of ungrazed production in the exclosure. Production of the 11-day defoliation treatment, the most severe, was 71% of control production, indicating slightly more removal from the grazed pasture. Experimental defoliation was probably more severe than measured because human intrusion lowered control production.

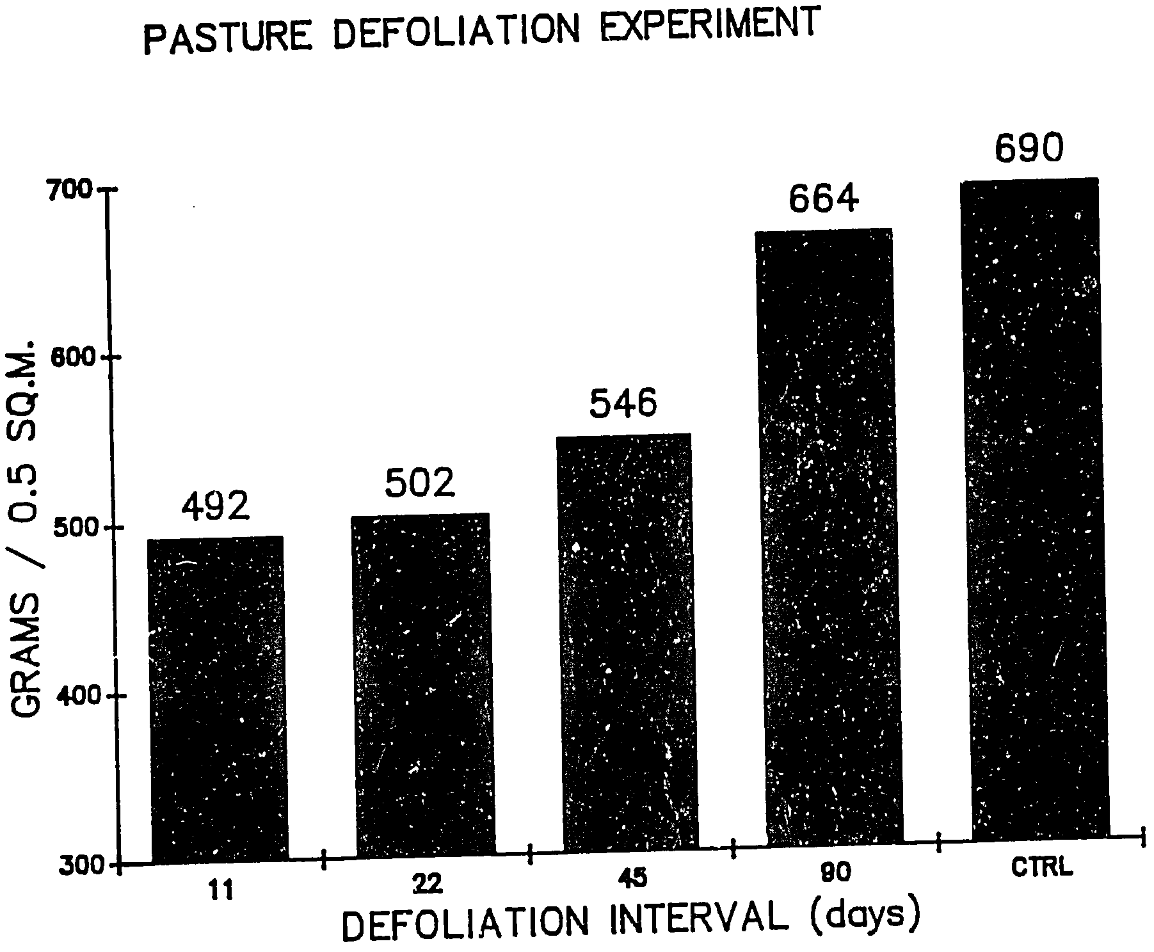

Fig. 30. Total biomass production per 0.5 m^2 plot for four defoliation treatments and a control inside an exclosure on the Hattisar pasture, Sauraha, Chitwan. Significant differences (p.05) detected between the combined first 3 treatments and the fourth treatment, and between the third and fourth treatment.

CONSUMERS

Elephant Consumption

Cut-Fodder Consumption.--the wet weight (WW) of fodder cut by elephant handlers showed a pronounced downward trend from June through April (Fig. 31A). The trend in dry weight (DW) biomass was reverse, however. Cut weight decreased by about 30%, but dry weight cut increased by some 45%. Linear regressions on both variables were significantly different than random expectation ($p \leq .001$). An average of 153 (± 11, alpha=.05) kg WW and 58 (± 4, alpha=.05) kg DW of grass fodder were cut daily for each elephant.

A year-long average of 25 (± 3, alpha=.05) kg dry weight fodder were consumed daily by the elephants. Consumption was roughly in proportion to its availability (Fig. 31B). Intake tracked availability from June through August, when consumption decreased and more fodder was rejected. Progressively less fodder was eaten and more rejected as grasses cured and quality decreased during the fall and early winter, and more tree fodder was offered. Mostly leaves and bark of trees were eaten, and the wood was discarded; this may account partially for the rise in leftovers.

Consumption increased rapidly during January when grasses initiated regrowth and a greater proportion of the fodder became palatable (Fig. 31B). The total amount of cut fodder remained relatively unchanged, however, because most of the biomass was in relatively unpalatable stems. Until June, fodder was primarily mature unburned stems with a flush of new leaves. Consumption increased after June as the proportion of new leaves and stems in the fodder increased. Handlers switched to new growth, stems and leaves, with a high wet weight during June.

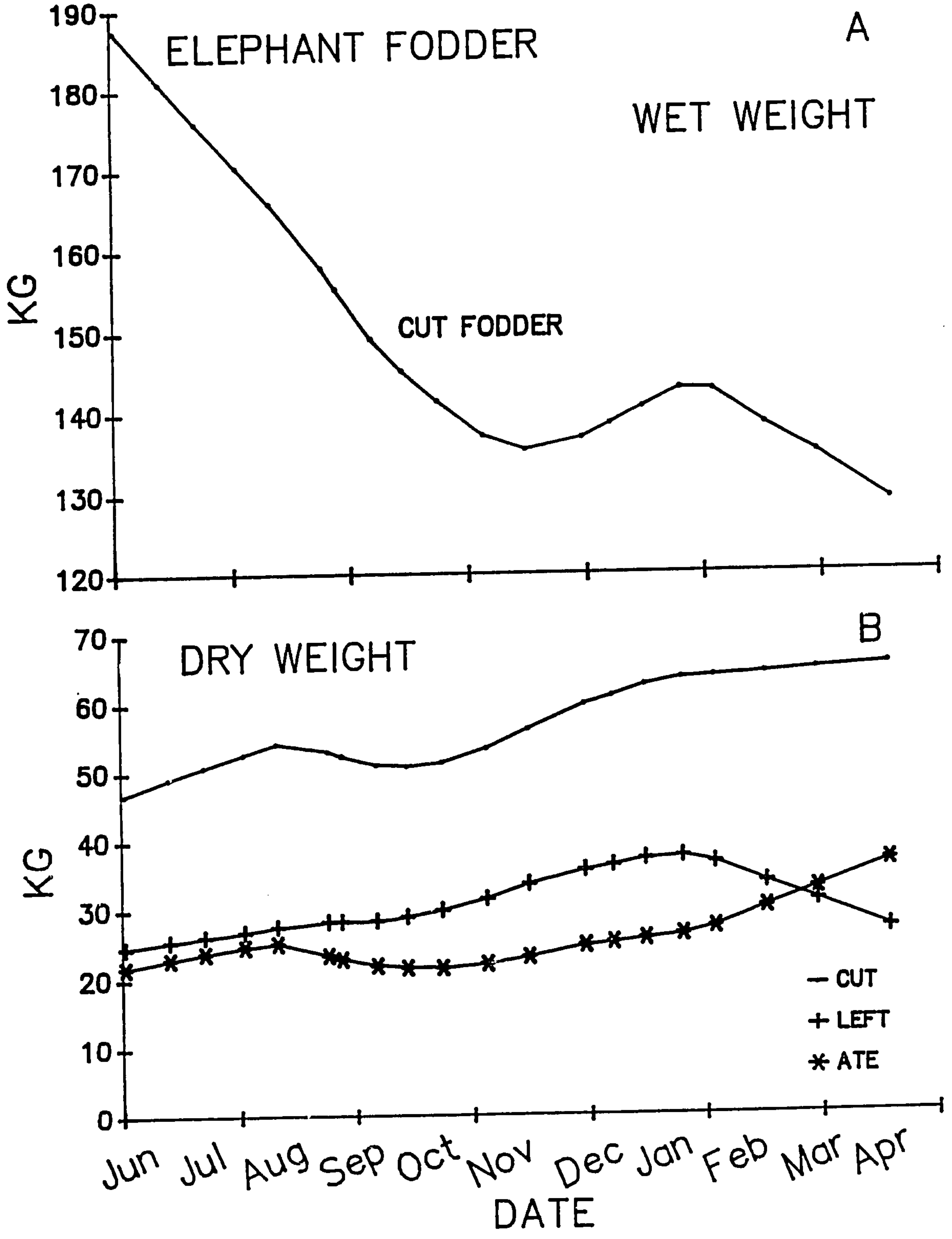

Fig. 31. Fodder data for 5 elephants at the Sauraha research camp from June 1986 through April 1987. *A*) Wet weight of cut fodder presented to elephants; *B*) Dry weight of cut fodder, amount leftover (not consumed), and amount eaten.

The cross-over of leftovers and eaten fodder curves is largely an artifact of the last sample's influence on the scattergram smoothing algorithm (Fig. 31B). The values shown in the figure are weighted values calculated by the scattergram smoothing algorithm (Lowess), not means. The actual mean weight of leftovers for the second to last sample was slightly greater than consumption; the relationship was reversed in the last sample, which did have greater consumption than leftovers.

Fodder Species.--counts of elephant-fodder species indicated that 80% of the biomass served to elephants was *Saccharum spontaneum* (Table 13). *Saccharum bengalense* and *Saccharum arundinacea* were used largely during the late monsoon and early fall when *Saccharum spontaneum* was in flower and other species of *Saccharum* were not. Handlers claimed that *Saccharum spontaneum* is less palatable when in flower. *Narenga porphorycoma* and *Themeda arundinacea* were used during the spring when the fast-growing shoots are most palatable. Mature stalks of corn (*Zea mays*) were fed to elephants during the late summer after the corn harvest. Senescent banana stems (*Musa balbisiana*) were occasionally fed to the elephants.

Bombax ceiba was an important tree-fodder species throughout most of the year, but principally during the fall and early winter when grass is least palatable. Handlers try to serve some tree fodder to elephants occasionally throughout the year to vary the diet. Other tree fodder species used *were Acacia catechu, Spondia pinnata,* and *Ficus* spp.

Grazing Intake.--grass intake by free-foraging elephants varied markedly over the year (Fig. 32). Dry-weight (DW) consumption was lowest at about 320 g 5-min^{-1}. sample during June, but rose linearly through the summer growing season to a peak of about 460 g 5-min^{-1} sample in October (Fig 32D). Thereafter,

Table 13. Monthly percentages of principal grass and tree fodder species fed to domestic elephants at Sauraha during 1985 and 1986. The number of samples varied because elephants were moved permanently or temporarily for work. SASP=*Saccharum spontaneum*; SABE=*Saccharum bengalense*; SAAR=*Saccharum arundinaceum*; NAPO=*Narenga porphorycoma*; BOCE=*Bombax ceiba*.

	Species					
Month	SASP	SABE	SAAR	NAPO	BOCE	N
June '85	73	0	25	2	0	114
July	98	0	2	0	0	124
August	95	3	0	0	3	74
September	61	0	32	0	7	116
October	75	13	2	0	11	95
November	92	0	2	0	7	59
December	81	0	4	0	15	26
Jan. '86	79	0	0	0	21	42
February	88	0	0	0	13	8
March	100	0	0	0	0	14
April	44	0	0	38	19	32
Mean %	80		2	10	2	6
					Total N	660

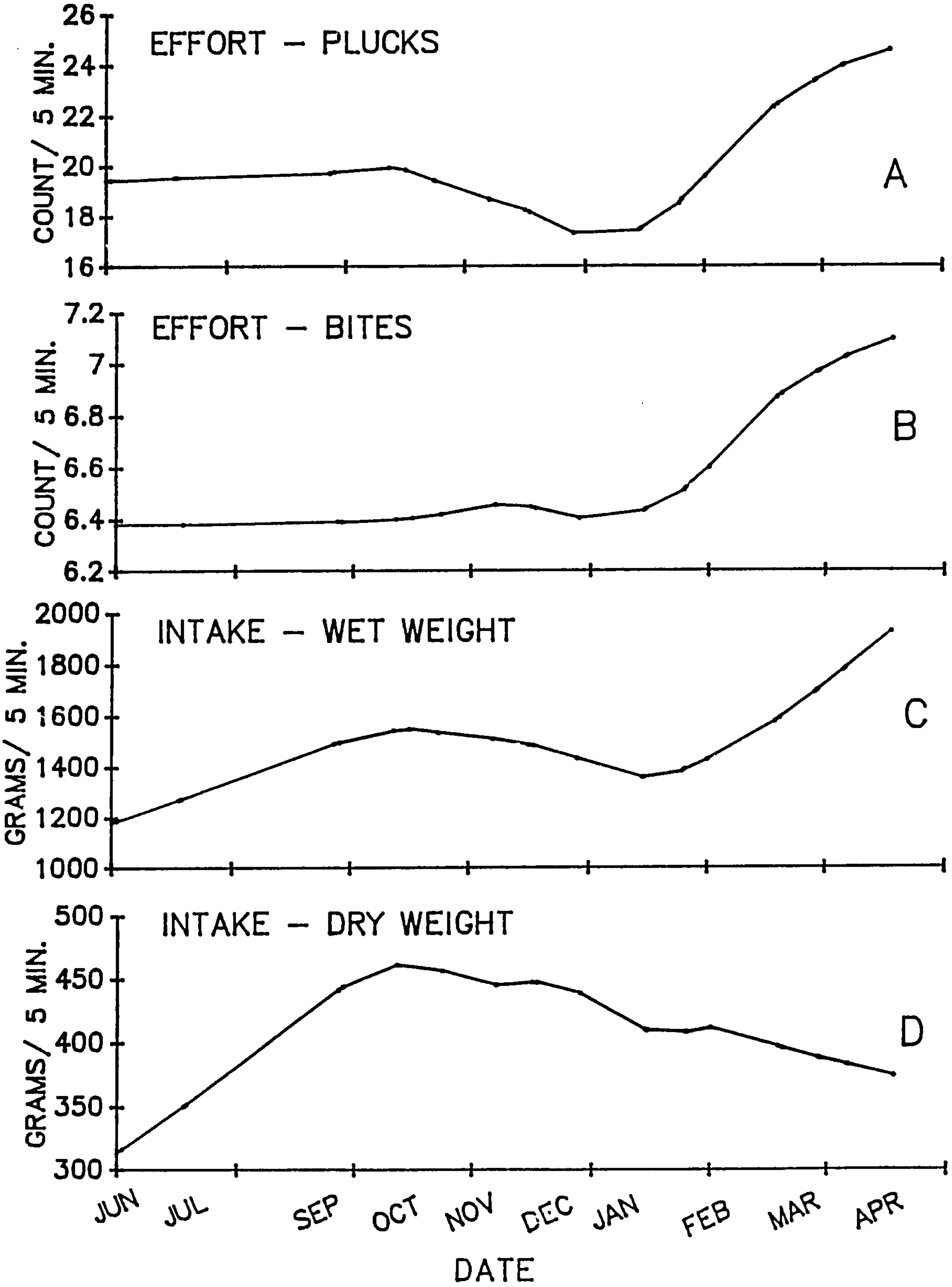

Fig. 32. Grazing data for 5 elephants at the Sauraha research camp from June 1986 through April 1987. *A*) effort measured by plucks of forage per 5 min. observation sample; *B*) effort measured by bites of forage per sample; *C*) wet weight of forage eaten per sample; *D*) dry weight of forage eaten per sample.

intake declined through April at a nearly constant, but slower rate. Mean DW intake was 415 g 5-min^{-1}. sample (± 61, alpha=.05). Mean daily consumption, assuming 4 hours of grazing per day, was about 20 kg DW.

Intake began declining as forage quality dropped at the end of the growing season in early October. Effort, as measured by "plucks", declined during October with intake(Fig 32A). Bite (ingestion) rate increased only very slightly during that time (Fig. 32B). Effort and WW intake increased rapidly during the first quarter of the year when regrowth occurred in response to fires. Dry weight intake, however, continued to decline.

Daily intake from both fodder and grazing increased rapidly during the summer when forage quality and quantity were highest (Fig. 33). Total consumption leveled during August, when grasses began to mature, as a result of lower fodder consumption. Intake remained relatively constant through the fall but began to increase rapidly during January. Intake climbed fast through late winter and spring, largely from increased fodder consumption.

No significant changes in elephant condition as measured by morphology, occurred during the year-long study.

Human Consumption

Grass cutting permit sales indicated that about 60,000 people annually came to the Park to cut grass during the 2-week January harvest season. Visitation was calculated to be over 216,000 visitor-days. An estimated 6,406 metric tons of *Imperata cylindrica* thatch grass and 4,726 metric tons of tall-grass reeds (flowering culms) were removed from the Park. The gross value of *Imperata cylindrica* thatch and tall-grass reeds were approximately NR 4.6 million (US $207,000) and NR 5.4 million (US $245,000). Subtraction of labor and permit

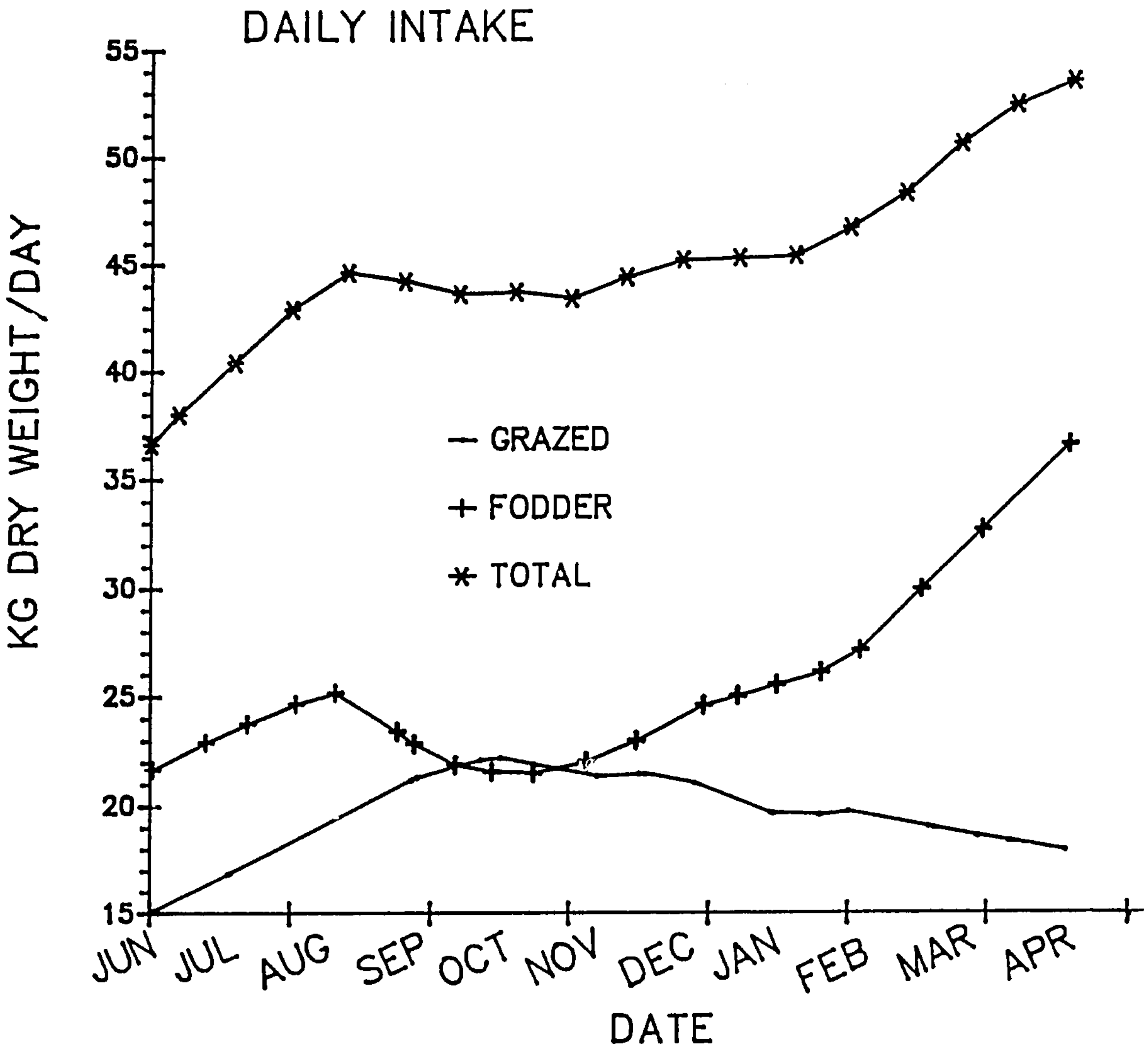

Fig. 33. Daily intake by 5 elephants at the Sauraha research camp from June 1986 through April 1987.

costs yielded a total net value of NR 5.5 million (US $250,000) to the local economy .

The value of Park grass to individual villagers was estimated as the cost of replacing grass materials with other structural materials. Individual village families save about NR 2000 (US $90) in costs for thatching material, and about NR 500 (US $25) for building canes compared to what they would pay for other materials to build a house. Alternate products available in the market were not considered affordable substitutes by more than 75% of the villagers responding to our questionnaire.

Villagers' attitudes toward the Park were becoming more positive as they began to realize that the Park is a valuable, needed source of managed resources that are not so easily, or not at all available elsewhere. Complete results of the thatch grass survey and attitudes questionnaire are found in Lehmkuhl et. al. (1988).

MODEL PREDICTIONS OF LANDSCAPE PRODUCTION

Predictions of general biomass production can be made from trends in grassland type areas simulated by the model (Fig. 7), if production per ha is assumed to remain constant. The supply of *Saccharum spontaneum* will nearly double, whereas the supply of other tall cane grasses, such as *Saccharum bengalense* and *Narenga porphorycoma*, will decline 5% over the next forty years as mixed tall grass and Woodland areas decrease. Supplies of *Imperata cylindrica* should remain fairly constant. *Imperata* from the *Themeda-Imperata* type will increase by a few tens of hectares as part of the residual *Imperata*-agriculture lands succeed into this type. The total supply, however, will decrease as some of the *Imperata*-agriculture lands succeed to tall grasses.

These trends are born out by the production subroutine of the model, which estimated consumption by animals and humans, and the residual biomass (Fig. 34). Consumption by both animals and humans is nearly linear over time for 20-year simulations. Elephant and human consumption are nearly constant because there is little information to suggest that current numbers of elephants of grass cutters will change. Grass cutters could increase if the supply of premium *Imperata cylindrica* grass was increased by management. The rhinoceros population increases with time in the model, but their forage consumption would have little effect on the large amount of available biomass.

Elephants and rhinoceros were estimated to consume about 10% of the 1987 *Saccharum spontaneum* biomass; humans removed about 5% of total production (Fig. 34C). About 9,000 tons of *Saccharum spontaneum* biomass are estimated to be available after elephant, rhinoceros, and grass cutting consumption is calculated. By 2001, about 15% more *Saccharum spontaneum*, 10,350 tons, will remain. These figures do not account for grass cut for sale as paper fiber because cutting for fiber had just begun during the study; remaining biomass calculated above would be available to harvest for paper fiber during the grass cutting season. *Saccharum spontaneum* harvest for paper fiber will likely increase dramatically unless constrained by management. Most of the *Saccharum spontaneum* biomass, and that of the mixed tall grass and woodland types remaining after grass cutting, is burned by grass cutters and elephant handlers.

Mixed tall grass and woodland biomass trends show quite another pattern of consumption (Fig. 34B). Animals, mainly grazing elephants, consume about 4% of production; whereas, humans cut about 26% of the total biomass for canes. During 1987, an estimated 9,560 tons of mixed tall grass biomass remained after grass

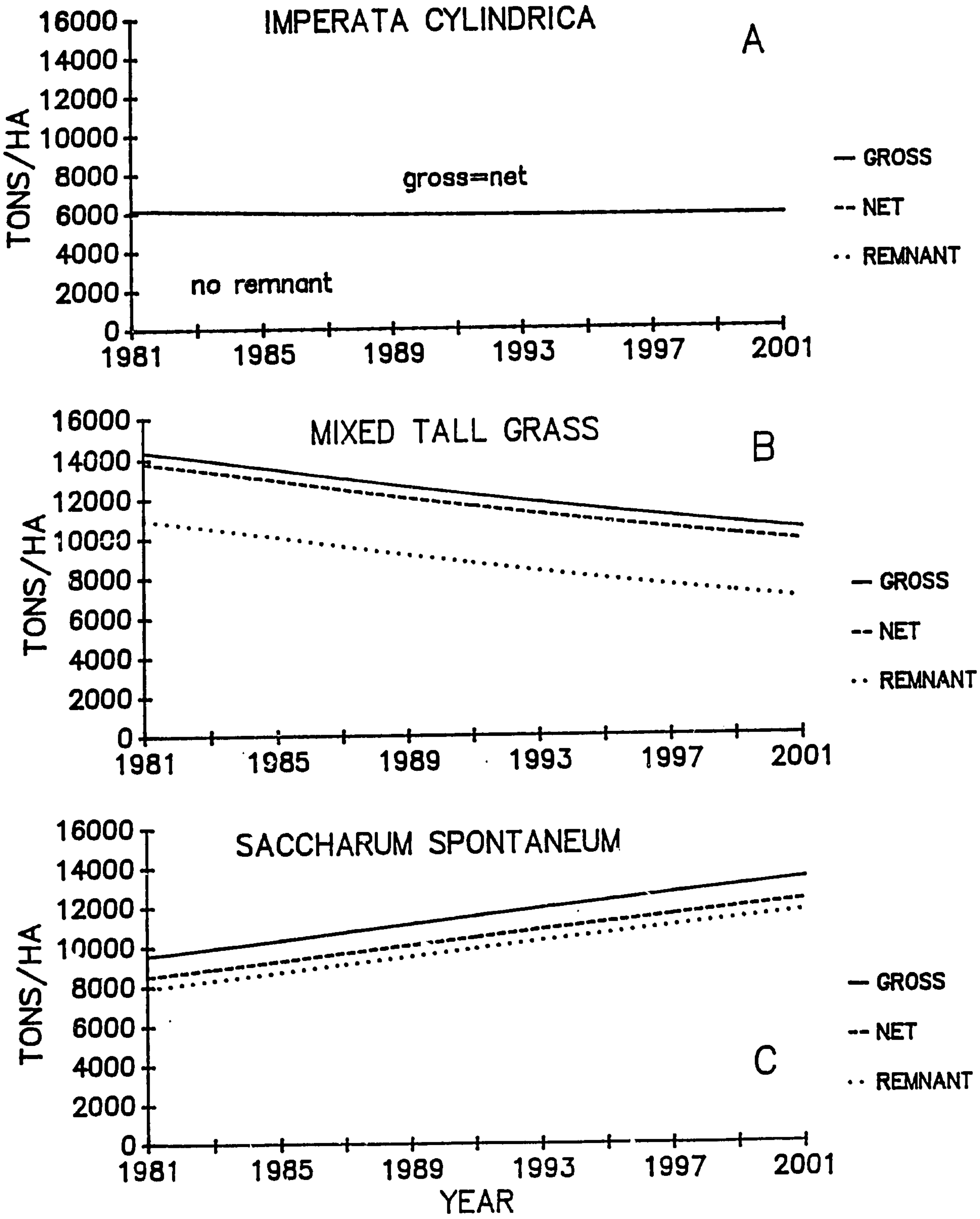

Fig. 34. Model estimates of biomass production in 3 major grassland types over 50 years. *A) Imperata cylindrica*; *B)* Mixed Tall Grass; *C) Saccharum spontaneum*.

cutting to fuel wild fires. An estimated 6,873 tons of biomass will remain in the year 2001.

Imperata cylindrica biomass is predicted to decline only about 2% over the next 20 years (Fig. 34A). Supplies will remain at about 5,800 tons, if the model assumption of no change in *Themeda-Imperata* areas to mixed tall grass holds true. The slight decline is due to the last remaining *Imperata*-Agricultural areas succeeding to tall grasses. Animal consumption of *Imperata cylindrica* was measured on the experimental production plots as 72 kg ha^{-1}, or 12% of total 1987 biomass. I assumed that all *Imperata cylindrica* would be cut by villagers; my experience was that the current biomass supplies very little of the demand for thatch grass.

DISCUSSION

GRAZING EFFECTS

Imperata cylindrica

The effects of grazing on *Imperata cylindrica* production varied with the season of burning. A significant difference was not detected for the apparent early-burn grazing effect during the two months after burning. Nevertheless, the caged clip-plot technique estimated the removal of 0.141 kg m^{-2} biomass, and grazing was evident from the clipped blades of grass.

Production and consumption estimates calculated with the cage-plot technique should be treated with caution. Several studies have shown higher growth rates inside cages and fences than outside (Colinshaw 1955; Grelen 1967) and overestimation of production (Allison and Kothman 1979; Sharrow and Motazedian 1983), especially under conditions of high temperature and fair weather (Heady 1957). Some studies have demonstrated underestimation of production (Dobb and Elliot 1964). Negative intake calculated for the third and fourth sample periods would indicate that production rate inside the fence was depressed, and estimates of consumption and production for *Imperata cylindrica* are conservative.

Grazing was short-lived on early burns compared to late burns. The area surrounding the plots was burned early, which is the norm, and a superabundance of forage diffused grazing pressure; grazers were not able to crop grazing lawns faster than the growth rate after early burning. However, late burns provided a flush of new growth much more palatable that surrounding vegetation. Imperata cylindrica foliage crude protein levels are three times higher immediately after fire than one month later, and five times higher than unburned foliage (E. Dinerstein, unpubl.. data). Grazers cropped the late-burn sward low into a grazing lawn (McNaughton 1984), maintaining high-quality growth stages for a longer period than if uncropped (Old 1969; Younger 1972; Haferkamp 1982).

I observed that grazers preferentially cropped late-burn plots, with clipped and burned foliage, over clipped and unburned foliage. It is well established that burning increases the nutrient quality of regrowth (Daubenmire 1968; Lemon 1968; Smith et. al. 1960; Vogle 1974; Allen et. al. 1976; McAtee et. al. 1979); but, the difference could be the effect of comparing biomass of different ages (Gillon 1983). Christensen (1977) controlled for tissue age in testing the hypothesis that burned foliage has higher nutrient value than unburned foliage. He found higher nitrogen, calcium, and magnesium in burned and clipped vs clipped-only foliage. He did not find a significant difference in foliage potassium and phosphorus.

Unburned plots showed no evidence of grazing. Herbivores probably found it much easier to forage in burned areas where new growth was unobstructed by the mat of dead leaves on unburned plots. Even if unburned regrowth had been readily available, herbivores would probably have chosen to forage on burned sites where foliage had three times more crude protein (E. Dinerstein, unpubl. data). Grazers were very selective in foraging on burned and clipped *vs* clipped-only forage, as discussed earlier.

Grazed, early-burn ANPP was estimated by adding herbivore consumption estimates to peak biomass. Grazed and ungrazed ANPP were nearly equal (Table 6), which suggested that grazing did not reduce or increase ANPP on early burns, i.e., *Imperata cylindrica* fully compensated (Belsky 1986a) for grazing. *Imperata cylindrica* is generally considered to do poorly under heavy grazing (Hubbard et. al. 1944; Ivens 1983; Andrews 1983), but less is known of the production response to moderate grazing. Chodakar (1977) demonstrated that the highest production and foliage nitrogen occurred at an intermediate level of defoliation (every 6 weeks), which would indicate overcompensation (Belsky 1986a), or grazing optimization (McNaughton 1979a; Hilbert et. al. 1981; Dyer et. al. 1982). However, the experiment was unreplicated (Chodakar 1977), and the results should be accepted with reservations.

The pasture defoliation experiment demonstrated that defoliation decreased production (under-compensation) on the pasture (Fig. 30). However, the pasture experiment is not entirely comparable with *Imperata cylindrica* production in the fire and grazing trials. *Imperata cylindrica* was only 23% of the pasture composition, but 100% of the trial plot composition. Also, clipping may not adequately simulate grazing; experimental clipping has been shown to have a greater negative effect on production than real grazing (Stroud et. al. 1985;

Johnson and Parson 1985). However, that does not negate the usefulness of the pasture defoliation experiment for assessing the defoliation effects and managing pastures for grass cutting or grazing.

ANPP on late-burn, grazed plots was not estimated (Table 6), because caged clip plots were not used to measure grazing effects (Milner and Hughes 1968; t'Mannetje 1978). An approximation of potential grazed ANPP would be that of ungrazed plots (956 g m^{-2}), assuming that plants fully compensated for grazing, as with early-burn plots. Herbivore consumption would be 363 g m^{-2}. These estimates should be accepted with caution for reasons concerning caged plot reliability as discussed above.

Narenga porphorycoma

The absence of a grazing effect was not unexpected for the *Narenga porphorycoma* mixed tall grass type. Caged plot comparisons and examination of plots for signs of grazing suggested little or no grazing. Animal density is low during most parts of the year (Mishra 1982a), and dense stands of tall fibrous grass with poor herbaceous understory have little palatable forage within reach of most herbivores. Grazing mostly occurs for several months after burning (Mishra 1982a). However, forage biomass is superabundant after burning, and the relatively few herbivores appear to have little influence on stand structure or production.

Saccharum spontaneum

There was a large apparent grazing effect on *Saccharum spontaneum* early and late-burn live weight between June and July (Fig. 24). This was puzzling. Village grass cutters were not active after mid-May, and elephant handlers were finding better fodder elsewhere. I would have guessed that rhinoceros grazing would be heaviest during the immediate post-fire period, which shows no consistent effect. However, Gyawali (1986) showed that rhinoceros consumption of *Saccharum spontaneum* is highest during the summer, with over 50% of the diet being *Saccharum spontaneum*.

A unavoidable problem with the design of these experiments to assess grazing impacts is the effect of necessary fire lanes in attracting grazers. Grass in fire lanes was allowed to grow until cutting was necessary to maintain recognizable plot boundaries, or prepare for the fire season. Cutting has similar stimulating effects on production (Lloyd 1972; Old 1972; Cable 1982; Detling and Painter 1983; but see Wallace 1987), so that fire lanes may have attracted grazers to the plots. I do not think this was a serious problem, however.

Nevertheless, the intrusion of grass cutters and elephant handlers did not allow an accurate assessment of grazing effects on *Saccharum spontaneum*. I concede "demonic intrusion" (Hurlburt 1985), which is unfortunate because the *Saccharum spontaneum* type was the most interesting site in terms of grazing. It is the primary foraging habitat for rhinoceros (Laurie 1978; Gyawali 1986), an important habitat for deer (Mishra 1982a), the principal fodder source for domestic elephants, and has high potential for paper fiber.

FIRE EFFECTS

Burning had significant effects on *Imperata cylindrica* and *Saccharum spontaneum* standing biomass, but not on *Narenga porphorycoma* biomass. For the first two types, early- burn biomass was significantly different than unburned biomass, but no different from late burning. Where early-burn and unburned treatments differed, late-burn biomass was considered different than unburned biomass by inference, but only when late-burn biomass was lower than early-burn biomass. Specific statistical comparisons between late and unburned biomass were generally not made to retain orthogonality of comparisons; a few comparisons were made at Bonferroni alpha levels, but tests were always non-significant because the alpha level was always very low.

Interpretation of significance tests for means of these time series data were complicated by the nature of the experiment. Late-burn plots had standing crops equal to unburned plots for the first 10 weeks before burning. After burning, biomass dropped rapidly, but re-growth was often immediate and sustained. The rapid drop and increase added a large amount of variability to the ANOVA, which tended to obscure tests for treatment differences. Also, unburned and late-burned plots had residual live and dead material, or already had begun to grow (*Imperata cylindrica* only) when the experiment started, so that initial biomass at the beginning of the experiment varied, introducing additional variation.

The time series were important for observing trends in standing biomass and the seasonal dynamics of production; but, results of significance tests often obscured the effects on ANPP, which was determined as the peak of the biomass curve. Data beyond the peak were not used for ANPP calculation, but were used in the ANOVA. For example, ANOVA for *Narenga porphorycoma* showed no significant difference between early- and late-burn total weight (Table 7). However, late-burn ANPP was less than half that of early-burn plots (Table 8), and the time series show a large difference (Figure 25).

ANPP for *Imperata cylindrica* in general may be overestimated by the experimental design relative to prevailing conditions. Usually all the *Imperata cylindrica* is cut by grass cutters before burning. Fires creep along in the litter and stubble remaining after cutting. My experimental plots, however, were not cut before burning, because I wanted to measure production without prior treatments. Fire temperatures were hotter, and more ash was deposited than would normally occur.

Production may be higher on the experimental plots than on outside areas because of greater nutrient availability from ash (Coutinho 1982). However, most studies have found that ash does not contribute directly to soil fertility, and that increased production following fire is generally caused by increased mineralization from higher soil temperature (Waksman 1927; Weaver and Rowlands 1952; Kucera and Ehrenreich 1952; Old 1969; Lloyd 1972; Vogle 1974; Wright and Bailey 1982; Daubenmire 1968; Hulbert 1988; among others), or elimination of canopy interception of precipitation by litter (Seastedt 1985). Burning, however, sometimes has negligible effects on some grasses (Coutinho 1982), or always reduces production in others (Smith 1960; Kucera 1981).

High fire temperatures on the unclipped experimental plots, however, may have reduced production, presumably by damaging below-ground parts (Aristeguita and Medina 1966). However, fire temperatures generally are not sustained in the absence of woody litter (Daubenmire 1968), and cause little damage to crowns, below-ground structures and seeds (Pitot and Mason 1951, in Daubenmire 1968; Daubenmire 1968; Vogle 1974; Wright and Bailey 1982), particularly below 1 cm depth (Wright and Bailey 1982).

Damage was not likely on my plots. Soil temperatures on experimental plots 1 cm below ground were less than 66° C during burning (the lowest temperature I was able to measure) (unpubl. data), and the ground was cool to the touch immediately after fire passage. Subsurface temperature was probably much less than 66°C, because soil moisture was high and fire spread rapid (Daubenmire 1968;

Vogle 1974), about 1 m min^{-1}. Soil temperatures were probably not high enough to damage rhizomes.

I do not think that production was elevated by not clipping prior to burning. Some parts of the ungrazed plots were cut by villagers prior to burning, and I later had a difficult time distinguishing uncut from cut areas for biomass sampling.

Early burning before substantial growth has begun can increase production (Moore 1960; San Jose and Medina 1975; Brockington 1961), or reduce production in relation to late burning (Afolayan 1978; Edroma 1984). The effect of burning season on ANPP varied among Chitwan grass types. The difference in ANPP (total weight estimate) between early and late burning of ungrazed *Imperata cylindrica* was small (Table 6); but, burned production was more than double the unburned production. Production of burned *Imperata cylindrica* has been reported as 4960 kg ha^{-1} in New Guinea (Chodakar 1977), and 4192 kg ha^{-1} in northern Thailand (Falvey et. al. 1981). This compares poorly to production in Chitwan of 11,720 kg ha^{-1} (early burn) and 9,560 kg ha^{-1} (late burn), but favorably with 4,400 kg ha^{-1} for unburned plots.

Production (total weight) of *Narenga porphorycoma* was highest on the early burns, intermediate on unburned plots, and lowest on late burns (Table 8). *Saccharum spontaneum* showed still another pattern; early and unburned production (live weight) were similar, whereas late-burn production was about one-fifth their value (Table 10). I could not discover any references in the literature with which to compare *Narenga porphorycoma* and *Saccharum spontaneum* ANPP.

In all cases, production on plots burned early during mid-February was equal to or greater than other burning treatments. Post-burn production rates were positive on early burns; whereas, production rates on unburned plots were zero, except for *Imperata cylindrica*, which had a low, positive growth rate. The lowest production occurred after late burning with the *Narenga porphorycoma* and *Saccharum spontaneum* types, but was lowest on unburned plots with *Imperata cylindrica*.

The beneficial effects of early burning were due perhaps to high soil temperatures during the beginning of the growing season. Ash may provide some nutrients that increase production (Coutinho 1982), but much of the nutrients in plant biomass are volatilized (nitrogen, phosphorus, and sulphur) or lost as particulate matter (calcium, potassium, and magnesium) to the atmosphere (Christensen 1977, Villecourt et. al. 1979; Gillon 1983; Jones 1985). However, soil organic matter transformations often increase as a result of high soil temperature, with oxidation of nitrification inhibitors, and increased cation availability (Jones 1985). The resulting increase in soil nitrate and ammonium concentrations stimulate plant growth (Wright and Bailey 1982).

Soil moisture was not affected by burning. The effects of defoliation, grazing and burning, on soil moisture and productivity have been variously reported; usually there is gradient of effects with less effect in mesic grasslands, than in more arid grasslands. McNaughton (1979a, b; 1983a; 1985a, b; 1986) claimed that grazing increases soil moisture by the removal of transpiring leaf surfaces. San Jose and Medina (1975) reported this effect after burning in Venezuelan llanos. Belsky (1986a) disputed McNaughton's claims with observation of greater vigor in ungrazed plants. Ellison (1960) claimed that grazing encourages drying of soil by evaporational loss. Athias et. al. (1975) found lower moisture in burned plots in the Lamto savanna than in unburned plots.

PATTERNS OF ANPP

Maximum estimates of ANPP for the three sites were surprisingly similar. *Narenga porphorycoma* (total weight estimate) and *Saccharum spontaneum* (live weight estimate) production were very close to 1.6 kg m^{-2} (16 t ha^{-1}). This value is higher than the maximum biomass estimates reported for 48 of 52 temperate and tropical sites reported by Coupland (1979). Reported values ranged from .086 to 3.406 kg m^{-2}. The four highest values were from "sub-humid" sites in India. Among the studies cited by Lamotte and Borliere (1983) in their review of savanna grassland production, fourteen sites in the dry savannas of east and south Africa generally produced less than 4 t ha^{-1} above-ground biomass; humid west African sites produced 8-12 t ha^{-1}; and South American savannas produced from 2-9 t ha^{-1}, but 10-25 t ha^{-1} in flooded grassland. Grass production in Chitwan is not the highest in the world as hypothesized, but nearly so.

I assume that the values reported by Coupland (1979) are dry weight. Wet weight production in Chitwan is about three times greater than dry weight; maximum wet weight production is 4.6 kg m^{-2}, which surpasses reported values. Another point to consider in comparing reported ANPP is that the various methods used to calculated ANPP are not always comparable, and will often give different results with the same data (Singh et. al. 1975; Lauenroth et. al. 1986).

Production of *Imperata cylindrica* was about 30% less than the tall grasses. Considering the difference in heights, about 1 m for *Imperata cylindrica* and 4-6 m for tall grasses, *Imperata cylindrica* ANPP was unexpectedly high. The difference, of course, is in the characteristic growth form. *Imperata cylindrica* is a sod-forming species that grows in dense swards. *Saccharum spontaneum* and *Narenga porphorycoma* have a clumped habit with wide spacing between clumps. From a ground-level, or basal area, perspective, the tall grasses are not particularly dense; it is only when standing, or attempting to walk through a stand that one perceives the stands to be dense.

Imperata cylindrica biomass peaked during the early summer on unburned plots, but production continued through October on burned plots. Growth peaks were probably regulated by availability of light or nutrients, as soil moisture seemed to be adequate during the summer. *Imperata cylindrica* is known to be very susceptible to shading; perhaps the dead material on the unburned plots shaded the surface sufficiently to depress surface temperature, nitrogen mineralization, and growth from basal meristems (Weaver and Rowlands 1952).

Saccharum spontaneum early and late burn production peaked during the early summer; but, *Narenga porphorycoma* production for the same treatments peaked later in the summer. This staggered pattern may be the result of allocation of resources to reproductive structures (Jones 1985; Larcher 1983). *Saccharum spontaneum* flowers during late September, but *Narenga porphorycoma* flowers later during November. Low production of late-burn *Narenga porphorycoma* and *Saccharum spontaneum* may have been the result of excessive leaf area removal, removal of apical meristems, severe depletion of carbohydrate reserves, and reduction in the number of live tillers (Jones 1985).

Soil moisture did not appear well correlated with changes in production rates. High rates of production occurred on early-burn plots during the spring despite the drop in soil moisture, particularly with *Imperata cylindrica*. Mixed tall grass production, however, appeared to increase during the late spring when pre-monsoon rains began to increase soil moisture. A similar, but more pronounced, effect of soil moisture was shown by *Saccharum spontaneum*. Early-burn production (live weight) seemed correlated with increasing spring soil moisture. Unburned production jumped during the summer when soils were wettest.

ELEPHANT CONSUMPTION

Fodder Consumption

The slope and shape of the fodder-weight curves were determined by the phenological change in biomass dry weight, and the fact that handlers generally cut a constant volume of grass (Fig. 31A, B). Handlers began to cut the current years growth of grass during June when it reached a size and density that was economical to cut. This grass had a low dry weight percentage. Prior to June, handlers cut the previous year's growth of grass which had a high dry weight. The dry weight ratio increased rapidly from June through the summer growing season, and then increased more slowly as mature grasses dried. The change in dry weight ratio was asymptotic, which accounts for a rapid change in the cut-fodder curves, followed by slower change.

The dip indicated in Figure 31A is probably a consequence of late monsoon floods in September and the Nepali holiday season. Access to good quantities of quality grass was limited by flood waters. During the holidays, half the staff was given a two week holiday and the remaining staff did double duty. Handlers probably cut less fodder per elephant at that time. The middle portion of both curves would be higher if not for these factors.

Grazing Consumption

Wet-weight and dry-weight intake curves are nearly symmetrical through January, indicating selection for succulent grass parts, as wet weight of available field biomass declined during the summer (Fig. 32). The curves diverged by February; wet weight increased while dry weight continued to decrease. The disparity is explained by the interaction of forage dry-weight percentage and foraging effort.

Grass dry weight decreased in general during that time as regrowth began, so that lower, or level, DW intake could be expected despite increased WW consumption. Foraging effort, however, increased in an apparent logarithmic fashion, probably because regrowth was difficult to pluck from among the mass of dead unburned or burnt material. Increased grazing effort was necessary to maintain even a declining DW intake; increased effort did not compensate for the decrease in dry-weight, much less increase DW intake. A deflection point in the effort rate appeared at that time in late February when fire had burned most of the grassland and significant growth had made for easier foraging. Foraging effort began to slow as the new/old biomass ratio increased with the growing season.

Forage quantity appeared to limit consumption during the late summer, fall, and early winter before fires when fodder or grazing intake declined (Fig. 33). Morphological measurements of the elephants, however, did not indicate any decline in body condition during that time (unpub. data). The apparent year-round good condition of the elephants was likely due to their regular diet supplements. Elephants were fed a 12 kg daily supplement of unhusked rice spiced with salt and molasses.

Diet supplements, and control of food habits and foraging behavior by handlers maintains good body condition in domestic elephants. Further examination of the data in terms of forage fiber characteristics and nutritional quality would be revealing, but is beyond the scope of the present studies.

PRODUCTION MODEL EVALUATION

Production

The production model was a simple method for linking what was known of production and consumption with the model of landscape dynamics (Chapter II) to examine trends in biomass availability and consumption. The assumption of constant production is perhaps an unrealistic simplification. Production may vary with precipitation, but it would seem that the extremely high amount of rainfall would have to decrease drastically to reduce production. Water tables are generally high throughout the grassland area and substantial production occurs during the dry season after burning. Also, precipitation was lower than average during the study (Fig. 3), so that production rates in the model would be conservative.

Some kinds of disturbance also may change the rate of production. Grazing generally reduces the rate of production (Jameson 1968; Younger 1972; Belsky 1986a), although full compensation and possibly overcompensation can occur (Belsky 1986a). Undercompensation, or reduction in production, was detected with the defoliation experiment on a grazing lawn composed of the prostrate grazing-adapted species, *Chrysopogon asciculatus*, *Cynodon dactylon*, and *Imperata cylindrica*. *Imperata cylindrica*, however, apparently compensated fully for grazing on experimental field plots, as discussed earlier. More research is needed on grass responses to grazing.

Cutting grass for fodder will have a greater impact on landscape production than grazing. A larger proportion of the plant is usually removed by clipping than by grazers, and cutters usually are less discriminating in the plant parts removed, especially with regard to meristematic regions (Jameson 1968; Younger 1972; Jones 1985). *Saccharum spontaneum* plants, which supply 90% of the elephant fodder, undercompensate after cutting. Regrowth of *Saccharum spontaneum* that was cut for elephant fodder was measured on a series of plots as only 11% of full production. Tall grass cut at ground level for production experiments grew very little after clipping, but the effect seemed to last only for that growing season. Sites cut for fodder in one year were indistinguishable from uncut areas after one growing season.

Fire experiments showed that early burning increased production. The current fire regime results in nearly all the grassland burned within one or two months. Management may change, and delays in burning or fire suppression will reduce total production, as shown by field experiments, and grass availability. Less than annual burning would result in a large amount of tangled dead material in the stand, and it is unlikely that villagers will be able to harvest as much under those conditions as they do now.

Consumption

Estimates of above-ground biomass consumption by the dominant, large mammalian herbivores were 12% for *Imperata cylindrica* swards, 4% for *Narenga porphorycoma*, and 10% for *Saccharum spontaneum* grassland. Mean consumption for the study area, weighted by grassland type area, was 6%. These figures are consistent with reported consumption in grassland savannas. Consumption by large herbivores is generally considered to be less than 10% for most grasslands (Wiegert and Evans 1967; Slobodkin et. al. 1967; Lamotte and Bourliere 1983); but, values from 18% to 94% have been reported, primarily from East Africa (Sinclair 1975; Wiegert and Evans 1967; McNaughton 1985a). Production varies stochastically (McNaughton 1985a), however, and consumption estimates should be equally variable.

Model predictions of consumption are minimum estimates of above-ground consumption. Consumption was estimated for the two largest herbivores only, rhinoceros and domestic elephant, ignoring the smaller herbivores (deer, rodents) and insects for which data were not available. Rodents and insects did not appear very abundant, and there was little evidence of consumption by these herbivores. Rhinoceros alone are estimated to make up 80% of the large herbivore biomass (Seidensticker 1976); an even greater percentage of the herbivore community is represented in the model by the addition of domestic elephants. Moreover, of the four species of deer, only the hog deer is strictly a grassland species (Mishra 1982a, Dhungel 1985). Axis deer, the most numerous species (Mishra 1982a), are mixed feeders that primarily use riverine forest, then grasslands (Mishra 1982a).

Forage intake by rhinoceros calculated for the model was approximate. The lignin marker technique can give poor results depending on forage selection, lignin digestibility, and chemical changes in lignin chemistry (Milford 1957; Van Dyne et. al. 1980). Moreover, daily defecation rates and weights may vary during the year, and the proportion of grasses in the diet varies seasonally. Nevertheless, the method seemed adequate to estimate total annual consumption in the absence of better data, without introducing unwarranted complications in the procedure.

Elephant consumption was based on the best available data from field studies (this chapter). Limitations in the data are the use of an average four hours spent grazing, and an unknown percentage of browse in the grazing diet. Grazing time varies directly with the number of daylight hours, but elephants require a minimum of four hours grazing per day. Moreover, during longer days much of the time is spent resting (elephant and handler) in the shade. This is probably not a serious problem when consumption is averaged for the entire year.

I assumed that grazing consumption was all grass, because assessing browse consumption was beyond the scope and resources of the study. I would guess that the amount of browse in the grazing diet is similar to the 6% *Bombax ceiba* in the fodder diet.

Human consumption was probably slightly overestimated. The sample of grass cutters at Sauraha may not have been a representative sample from which to infer the total harvest. Cutters in other areas are known to cut little grass, and concentrate on stealing firewood hidden in grass bundles. However, 20% of the cutting permits were sold at Sauraha, and the largest grassland area occurs in this vicinity. The proportions of *Saccharum spontaneum* and other tall grasses from the Mixed Tall Grass type were not identified in the survey, so that the estimated 25% of grass removed from *Saccharum spontaneum* is crude, but probably liberal.

SUMMARY

The effects of fire and grazing on *Imperata cylindrica*, *Narenga porphorycoma*, and *Saccharum spontaneum* grassland swards were examined on experimental plots for one year. Fire and grazing had significant effects on standing biomass of *Imperata cylindrica*. Early burning, without grazing, produced the greatest biomass (1.2 kg m^{-2}). Late-burn production was 81% of early-burn production; unburned production was 38% of early burn production. Grazing removed the greatest biomass from the late-burn plots, probably because burned plots were surrounded by older and less palatable forage. A late-burn grazing effect appeared to last at least 15 weeks. Grazing after early burning removed an estimated 141 g m^{-2}, 12% of annual above-ground production. Humans harvested

nearly all of the remaining biomass during the January grass cutting season. The grazing effect lasted for about 10 weeks, when forage apparently became unpalatable. *Imperata cylindrica* probably compensated fully for grazing by producing biomass equal to ungrazed production. Model simulations indicated little change in *Imperata cylindrica* biomass availability over the next 20-years.

No significant fire and grazing effects were found with *Narenga porphorycoma* standing biomass. Grazing was not evident on burned or unburned plots. Early burning resulted in the highest above-ground production (1.6 kg m^{-2}), followed by unburned production (60%) and late-burn production (42%). Large herbivore consumption was estimated by model simulations as 4% of production. Humans harvested 26% of above-ground production during the grass cutting season. Model simulations indicated a 28% decrease in mixed tall grass biomass over the next 20 years due to succession and erosion.

Problems were experienced with the *Saccharum spontaneum* experimental plots. Villagers and elephant handlers surreptitiously cut grass from the plots, and ruin the treatment design. However, data were collected over the year to assess production in response to burning as best possible. Late burning appeared to decrease production to 22% of the early and unburned production (1.65 kg m^{-2}). Model simulations indicated that rhinoceros and domestic elephants consumed 10% of annual production, whereas, humans harvested 5 %. The model of landscape dynamics showed a 15% increase in *Saccharum spontaneum* biomass over the next 20 years.

Above-ground net primary production of Chitwan's grasslands appears to be among the highest in the world. Tall grass production was surpassed by only five of 70 grasslands reported in the literature. Large herbivore grassland consumption in the study area averaged 6% of above-ground production. The literature reports less than 10% consumption for most natural grazing systems, except the Serengeti.

Above-ground production of a village pasture, considered a surrogate for Park grazing lawns, was 872 g m^{-2}. Grazed production was 39% less than the ungrazed production of 1410 g m^{-2}, as measured inside an exclosure. Consumption by livestock was 100% of annual production. An experiment examined the effects of four frequencies of defoliation on pasture production. Defoliation reduced production in a nonlinear manner; defoliation every 11 days reduced production 29%, but defoliation every 90 days reduced production only 4%. These are minimum values because villagers cut a small amount of grass from the control plots. The grazed pasture composition was dominated by *Chrysopogon asciculatus* (45%), *Cynodon dactylon* (19%), and *Imperata cylindrica* (19%). The ungrazed pasture was quickly dominated by *Imperata cylindrica* after one year of protection from grazing.

Human harvest of grass products during the two weeks of the legal grass cutting season was surveyed. About 60,000 permits were sold, and there were 216,000 visitor-days. The harvest of thatch grass and canes for house construction was 6406 t and 4726 t, with monetary values of NR 4.6 million ($207,000) and NR 5.4 million ($245,000). Subtraction of labor and permit costs yielded a net value to the economy of NR 5.5 million ($250,000). Benefits accrued to the individual village family were NR 2,500 ($115). Seventy-five percent of the villagers interviewed were dependent on grass products from the Park for their subsistence needs.

Domestic elephant food intake and foraging behavior was studied for one year. An average daily fodder ration of 58 kg DW (153 kg WW) was cut for each elephant. Elephants consumed 25 kg DW fodder. Eighty percent of the fodder was the floodplain grass *Saccharum spontaneum*. Six percent was tree fodder, mainly the limbs of young *Bombax ceiba* trees. Elephants were grazed for at least four hours each day. Grazing consumption rate averaged 415 g 5-min^{-1} (DW), and daily consumption (4 hours) was 20 kg DW. Total consumption was estimated as 45 kg DW (135 kg WW). Intake increased during the summer, leveled during the fall through December, then increased through the remainder of the dry season. No significant change in body condition was detected by morphological measurements.

CHAPTER IV. CONCLUSIONS FOR MANAGEMENT

RIVER EROSION

The floodplain emerged as the dominant factor in landscape stability. Bank erosion inside and outside the Park contribute to an increasing area of floodplain habitat type, particularly *Saccharum spontaneum*. Despite questionable long-term (200-year) model predictions, short-term trends indicate a real problem; an average 2.6 ha of agricultural land has been lost each year between 1964 and 1981. Although inclusion of high-quality floodplain habitats in the Park is beneficial for Park uses, the gain is at the expense of subsistence farmers. Loss of agricultural lands to floodplain will be difficult to control given the volatile nature of the river channel, and the high cost of doing an effective job.

SUCCESSION

The increase in the *Saccharum spontaneum* type is good news for Park management. *Saccharum spontaneum* grassland is perhaps one of the highest quality habitats in the Park in terms of forage quality and use by wild herbivores (Mishra 1982a; Dhungel 1985). It is essential rhinoceros habitat (Laurie 1978), the major source of elephant fodder (80%), and is used heavily by the deer species (Mishra 1982a). The Park may be able to play a larger role in the local economy by providing *Saccharum spontaneum* for paper fiber, via grass cutting permits. Such a program would have to be carefully planned and managed, however, to not jeopardize wildlife conservation and other natural values.

The supply of tall grasses, other than *Saccharum spontaneum*, will decrease but biomass will be adequate to supply current demand. Demand is not likely to change unless new markets are found, or management of the grass cutting changes.

Imperata cylindrica biomass will decrease only very slightly. Demand is extremely high for this grass, and will continue to rise as local population and households increase. Judicious grassland management would not endanger, but could enhance, wildlife or plant conservation values, and increase total *Imperata cylindrica* biomass at little cost. A program to mechanically break up extensive tall grass stands that were formerly *Imperata cylindrica* into a patchwork of tall grass and *Imperata cylindrica* would benefit wildlife by increasing landscape diversity, it would increase thatch supplies, allow for better fire control and management by breaking up extensive stands of inflammable tall grass, and provide better opportunities for wildlife viewing.

FIRE MANAGEMENT

Staggered burning of grasslands in small patches could provide fresh, high-quality forage for a longer time during the dry season than at present. Laurie (1978) and Dinerstein (1979) have suggested this practice to increase carrying capacity for large mammalian herbivores in Nepalese reserves. Roy (1986) described a successful patch burning program in Manas Wildlife Sanctuary in Assam. Rodgers (1986) provided a good review of fire management for wildlife habitat management in south Asia.

Results of my fire experiments indicated that staggered burning may foster the formation of pasture-like grazing lawns by concentrating grazing pressure on limited areas. Grazing lawns would produce high-quality forage year-round, may decrease crop depredation by attracting wild herbivores away from agriculture, and would increase herbivore carrying capacity. Patch size would be critical for success; a patch to large would be hard for herbivores to crop fast enough to keep the grass short, and a patch too small might be overgrazed and not provide adequate benefits to warrant management.

Model simulations revealed that complete suppression of fire could have very different effects on the dynamics of succession to riverine forest, depending on how successional processes change. Riverine forest, the most productive and valuable habitat for wildlife, could increase or decrease with fire suppression, but in possibly different ways. Conventional thinking says that riverine forest would increase with fire suppression; but, my observations suggest that riverine forest could decrease instead. Further research is warranted to determine the how fire suppression may affect succession.

Patch burning would also increase cover for wildlife. Oliver (1980) concluded that widespread burning was one of the factors contributing to the decline of the endangered pygmy hog (*Sus salvanius*) (likely extinct in Chitwan) and hispid hare (*Caprolagus hispidus*). Roy (1986) claims that his patch burning program has been instrumental in increasing the population of pygmy hog in Manas, and managing high quality habitat for other species. Patch burning also would provide essential spring nesting habitat for grassland birds in unburned sites that are now missing with widespread, uncontrolled fire (Rodgers 1986).

PASTURE MANAGEMENT

Studies on the village pasture provide a base of data from which management studies and plans can be formulated. Although ungrazed pastures produced over 30% more forage than grazed pasture, the quality of ungrazed forage was lower (E. Dinerstein, unpubl. data), and the carrying capacity would likely be lower. There would be some point to manage for, where production and quality are optimum. This is just one point to consider to increase livestock production around the Park. A complete analysis of grazing management that considers forage production, forage quality, introducing forage crops, stall feeding, tree plantation intercropping, and grass responses to grazing is beyond the scope of present studies, but is recommended for proper management.

RESEARCH NEEDS

Research and management are not exclusive. Good management should also take a scientific approach to make the results more reliable and applicable to a wide range of sites and conditions. A list of priority research topics and questions should include:

1. Studies to examine large-scale floodplain dynamics for the entire Rapti River floodplain in the Chitwan valley. Remote sensing techniques would be ideal. LANDSAT images spanning 10 to 15 years are probably available for better estimating model parameters.
2. Effects of grazing and defoliation on production. How do grasses compensate for grazing? What are the effects on competitive and successional relationships?
3. What are the effects of climatic variation (rainfall and temperature) on annual production?
4. How does fire effect tree and woody shrub survival?
5. Will staggered burning through the dry season increase species diversity by providing critical hiding or thermal habitat for mammals, or nesting sites for grassland birds? Does staggered burning of *Imperata cylindrica* and tall grasses attract large herbivores away from agriculture and decrease crop depredation?

6. Investigate grassland management techniques that will increase landscape diversity and biomass production of *Imperata cylindrica* for wildlife and human consumption. Does the resulting higher landscape diversity increases wildlife populations, movements, or habitat selection?

LIST OF REFERENCES

Abrams, M.D., A.K. Knapp, and L.C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. Amer. J. Bot. 73: 1509-1515.

Afolayan, T.A. 1979. Change in percentage ground cover of perennial grasses under different burning regimes. Vegetatio 39: 35-41.

Allen, L.J., L.H. Harbers, R.R. Schalles, C.E. Owensby, and E.F. Smith. 1976. Range burning and fertilizing related to nutritive value of bluestem grass. J. Range Manage. 29: 306-308.

Allison, C.D., and M.M. Kothman. 1979. Effects of level of stocking pressure on forage intake and diet quality of range cattle. Proc. West. Sect. Amer. Soc. Anim. Sci. 30: 174-178.

Andrews, A.C. 1983. *Imperata cylindrica* in the highlands of northern Thailand its productivity and status as a weed. Mount. Res. and Develop. 3: 386-388.

Aristeguita, L., and E. Medina. 1966. Proteccion y quema de la sabina llanera. Bol. Soc. Venez. Cienc. Nat. 26: 129-139.

Athias, F., G. Josens, and P. Lavelle. 1975. Influence de feu de brousse annuel sur le peuplement endoge de la savane de Lamto (Cote de Ivoire). Proc. 5th Int. Coll. Soil Zoology, Prague, 1973 : 389-397.

Babu, C.R. 1977. Herbaceous Flora of Dehra Dun. Publications and Information Direc, New Delhi. 721 pp.

Badam, G.L. 1984. Pleistocene faunal succession in India. Pages 746-776 in Whyte, R.O. (ed.) (*q.v.*).

Badgely, C. 1984. The paleoenvironment of South Asian Miocene hominids. Pages 787-795 in Whyte, R.O. (ed.) (*q.v.*).

Bazzaz, F.E., and J.A.D. Parrish. 1982. Organization of grassland communities. Pages 233-254 in Estes, J.R. et. al. (*q.v.*).

Beard, J.S. 1967. Some vegetation types in tropical Australia in relation to those of Africa or Amazonas. J. Ecology 55: 271-290.

Belovsky, G.E. 1984. Herbivore optimal foraging: a comparative test of three models. Am. Nat. 124: 97-115.

Belovsky, G.E. 1986. Optimal foraging and community structure: implications for a guild of generalist herbivores. Oecologia 70: 35-52.

Belsky, A.J. 1985. Long-term vegetation monitoring in the Serengeti National Park, Tanzania. J. Appl. Ecol. 22: 449-460.

Belsky, A.J. 1986a. Does herbivory benefit plants? A review of the evidence. Am. Nat. 127: 870-892.

Belsky, A.J. 1986b. Population and community processes in a mosaic grassland in the Serengeti, Tanzania. J. Ecology 73: 841-856.

Belsky, A.J. 1986c. Revegetation of artificial disturbances in grasslands of the Serengeti National park, Tanzania. I. Colonization of grazed and ungrazed plots. J. Ecology 74: 419-437.

Belsky, A.J. 1986d. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. II. Five years of successional change. J. Ecology 74:.

Belsky, A.J. 1987a. The effects of grazing: confounding of ecosystem, community and organismal scales. Am. Nat. 129: 777-783.

Belsky, A.J. 1987b. Revegetation of natural and human-caused disturbances in the Serengeti National Park, Tanzania. Vegetatio 70: 51-60.

Bharucha, F.R. 1975. Fifty years of ecological and phytosociological research in India. Vegetatio 30: 153-155.

Blanford, W. 1888. The Fauna of British India: Mammalia. Taylor and Francis, London. 617 pp.

Blasco, F. 1983. The transition from open forest to savanna in continental southeast Asia. Pages 167-181 in Bourliere, F. (ed.) (*q.v.*).

Bledsoe, L.J., and G.M. Van Dyne. 1971. A compartment model simulation of secondary succession. Pages 480-513 in Patten, B.M. (ed.). Systems Analysis in Ecology. Academic Press, New York.

Bolton, M. 1975. Royal Chitwan National Park Management Plan, 1975-1979. FO NEP/72/002, Project Working Document No. 2. U.N.D.P/FAO. of the United Nations. 105 pp.

Bor, N.L. 1953. Manual of Indian Forest Botany. Oxford University Press, Bombay. 441 pp.

Bor, N.L. 1960. Grasses of Burma, Ceylon, India, and Pakistan. Pergamon Press, Oxford. 767 pp.

Bormann, F.H. and G.E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York. 253 pp.

Bourliere, F. (ed.). 1983a. Tropical Savannas. Elsevier Scientific, Amsterdam. 730 pp.

Bourliere, F. 1983b. The savanna mammals: introduction. Pages 359-361 in Bourliere, F. (ed.) (*q.v.*).

Brandis, D. 1906. Indian Trees. Archibald, Constable, London. 767 pp.

Brockington, N.R. 1961. Studies on the growth of *Hyparrhenia*-dominant grassland in Northern Rhodesia. I. Fertilizer response, II. The effect of fire. J. Br. Grassl. Soc. 16: 54-64.

Burkhill, J.H. 1910. Notes from a journey to Nepal. Rec. Bot. Survey India 4: 59.

Cable, D.R. 1982. Partial defoliation stimulates growth of Arizona cottontop. J. Range Manage. 35: 591-593.

Carson, B., P.B. Shah, and P.L. Maharjan. 1986. Land Systems Report: The Soil Landscapes of Nepal. HMG Topological Survey Branch, Kathmandu, Nepal. 140 pp + appendices.

Caughley, G. 1969. Wildlife and recreation in the Trisuli watershed and other areas in Nepal. HMG/FAO/UNDP Trisuli Watershed Development Project. Project Report No. 6, Kathmandu, Nepal. 54 pp.

Caughley, G. 1976a. Wildlife management and the dynamics of ungulate populations. Appl. Biol. 1: 183-246.

Caughley, G. 1976b. Plant-herbivore systems. Pages 94-113 in May, R.M. (ed.). Theoretical Ecology. Sinauer, Sunderland, Mass.

Caughley, G., and J.H. Lawton. 1981. Plant-herbivore systems. Pages 132-166 in May, R.M. (ed.). Theoretical Ecology. Sinuaer, Sunderland, Mass.

Chadhokar, P.A. 1977. Establishment of Stylo (*Stylosanthes guianensis*) in Kunai (*Imperata cylindrica*) pastures and its effect on dry matter yield and animal production in the Markham Valley, Papua New Guinea. Trop. Grassl. 11: 263-272.

Champion, H.G. 1936. A Preliminary Survey of the Forest Types of India and Burma. Indian Forest Records, "Silviculture". Manager of Publications, New Delhi.

Champion, H.G., and S.K. Seth. 1968. A Revised Survey of the Forest Types of India. Publications Division, New Delhi. 404 pp.

Chew, R.M. 1974. Consumers as regulators of ecosystems: an alternative to energetics. Ohio J. Sci. 74: 359-371.

Christensen, N.L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. Oecologia 31: 27-44.

Clements, F.E. 1916. Plant Succession. Carnegie Inst., Washington. 512 pp.

Clutton-Brock, T.H., F.E. Guinness, and S.D. Albon. 1982. Red Deer: Behavior and Ecology of Two Sexes. University of Chicago Press, Chicago. 378 pp.

Cole, M.M. 1986. The Savannas: Biogeography and Geobotany. Academic Press, New York. 438 pp.

Cole, N.H.A. 1977. Effects of light, temperature, and flooding on seed germination of the neotropical *Panicum laxum* SW. Biotropica 9: 191-194.

Colinshaw, S.J. 1955. The effect of sampling cages on the yield of herbage. J. Brit. Grassl. Soc. 6: 179.

Collins, S.L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68: 1243-1250.

Collins, S.L., and S.C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64: 87-94.

Collinson, M.E., and A.C. Scott. 1987. Factors controlling the organization and evolution of ancient plant communities. Pages 399-420 in (ed.). Blackwell Scientific Publishers, Oxford.

Connell, J.H., and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Coupland, R.T. 1979. Grassland Ecosystems of the World: Analysis of Grasslands and Their Uses. Cambridge University Press, Cambridge. 401 pp.

Coutinho, L.M. 1982. Ecological effect of fire on the Brazilian Cerrado. Pages 273-291 in Huntley, B.J. and B.H. Walker (eds.). Ecology of Tropical Savannas. Springer-Verlag, Berlin.

Crawley, M.J. 1983. Herbivory: The Dynamics of Animal-Plant Interactions. University of California Press. 437 pp.

Cumming, D.H.M. 1982. The influence of large herbivores on savanna structure in Africa. Pages 215-245 in Huntly, B.J. and B.H. Walker (eds.). The ecology of tropical Savannas. Springer-Verlag, New York.

Dabadghao, P.M., and K.A. Shankarnarayan. 1973. The Grass Cover of India. Indian Council of Agri. Research, New Delhi. 713 pp.

Daubenmire, R. 1968. Ecology of fire in grasslands. Adv. Ecol. Res. 5: 209- 266.

Demment, M.W., and P.J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am. Nat. 125: 641-672.

Deshmukh, I. 1986. Primary production of a grassland in Nairobi National Park, Kenya. J. Appl. Ecol. 23: 115-123.

Detling, J.K., and E.L. Painter. 1983. Defoliation response of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 57: 65-71.

Dhungel, S.K. 1985. Ecology of the Hog Deer in Royal Chitwan National Park, Nepal. Ph.D. Diss., University of Montana, Missoula. 114 pp.

Dillewjin, C.V. 1952. Botany of Sugarcane. Chronica Botanica, Waltham, Mass.

Dinerstein, E. 1979. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part I: Vegetation, modifying factors, and successional relationships. Biol. Conserv. 15: 127-150.

Dinerstein, E. 1985. Just how many rhinos are there in Chitwan? Smithsonian-Nepal Terai Ecology Project Newsletter No. 2:5.

Dinerstein, E., and C.M. Wemmer. 1988. Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphorbiacea) in lowland Nepal. Ecology 69: 1768-1774.

Doob, J.L., and C.R. Elliott. 1964. The effect of pasture sampling cages on seed and herbage yields of creeping red fescue. Can. J. Plant Sci. 44: 96-99.

Donahue, R.L., R.W. Miller, and J.C. Shickluna. 1977. Soils: An Introduction to Soils and Plant Growth. Prentice-Hall Inc., Englewood Cliffs, NJ. 626 pp.

Drury, W.H., and I.C.T. Nesbit. 1973. Succession. J. Arnold Arboretum 54: 331- 368.

Dyer, M.I., J.K. Detling, D.C. Colemen , and D.W. Hilbert. 1982. The role of herbivores in grasslands. Pages 255-296 in Estes, JR. et. al. (*q.v.*).

Edroma, E.L. 1984. Effects of burning and grazing on the productivity and number of plants in Queen Elizabeth National Park, Uganda. Afr. J. Ecology 22: 165-174.

Egler, F.E. 1954. Vegetation science concepts, I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412- 417.

Eisenberg, J.F., and G.M. McKay. 1976. Comparison of ungulate adaptations in the New World and Old World tropical forests with special reference to Ceylon and the rainforests of central America. Pages 585-602 in Geist, V. and F. Walther (eds.). Behavior of ungulates in Relation to Management. IUCN, Morges, Switzerland.

Eisenberg, J.F., and J. Seidensticker. 1976. Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. Biol. Conserv. 10: 293-308.

Ellison, B.C. 1925. HRH The Prince of Wales's Sport in India. William Heinemann, London.

Ellison, L. 1960. Influence of grazing on plant succession of rangelands. Bot. Rev 26: 1-78.

Escolar, R.P., and F.W. Allison. 1976. Effect of water table depth on the yield of seven sugar cane varieties in Puerto Rico. J. Agric. Univ. P.R. 10: 228- 237.

Estes, J.R., R.J. Tyrl, and J.N. Brunken (eds.). 1982. Grasses and Grasslands: Systematics and Ecology. University of Oklahoma Press, Norman, Okla.

Eussen, J.H.H. 1979. Some competition experiments with Alang-Alang (*Imperata cylindrica* (L.)Beauv.) in replacement series. Oecologia 40: 351-356.

Eussen, J.H.H., and G.J. Nieman. 1981. Growth inhibiting substances from leaves of *Imperata cylindrica*. Z. Pflanzenphysiol 102: 263-266.

Eussen, J.H.H., and S. Wirjahardja. 1973. Studies of an Alang-Alang (*Imperata cylindrica* (L., Beauv.) vegetation. Biotrop Bulletin - Bogor, Indonesia. 24pp.

Falvey, J.L. 1981. *Imperata cylindrica* and animal production in south-east Asia: A review. Trop. Grassl. 15: 52-56.

Falvey, J.L., P. Hengmichai, and P. Pongpiachan. 1981. The productivity and nutritive value of *Imperata cylindrica* (L) Beauv. in the Thai Highlands. J. Range Manage. 34: 280-282.

Falvey, L., and P. Hengmichai. 1979. Invasion of *Imperata cylindrica* (L.) Beauv. by *Eupatorium* species. J. Range Manage. 32: 340--344.

Fortescue, J. 1912. The Royal Visit to India. MacMillan, London. 324 pp.

Frankland, B. 1981. Germination in shade. Pages 187-204 in Smith, H. (ed.). Plants and the Daylight Spectrum. Academic Press, New York.

Frodin, D.G. 1984. Guide to Standard Floras of the World. Cambridge University Press, Cambridge.

Gauch, H.G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge. 298 pp.

Gaur, R. 1987. Environment and Ecology of Early Man in Northwest India. B.R. Publishing Corporation, New Delhi. 252 pp.

Gee, E.P. 1959. Report on a survey of the rhinoceros area in Nepal. Oryx 5: 59-85.

Gillison, A.N. 1983. Tropical savannas of Australia and the southwest Pacific. Pages 183-244 in Bourliere, F. (ed.) (*q.v.*).

Gillon, D. 1983. The fire problem in tropical savannas. Pages 617-642 in Bourliere, F. (ed.). (*q.v.*).

Gleason, H.H. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 43: 463-481.

Glenn-Lewin, D.C. 1980. The individualistic nature of plant community development. Vegetatio 43: 141-146.

Grelen, H.E. 1967. Comparison of cage methods for determining utilization on pine-bluestem range. J. Range Manage. 20: 94-96.

Gumbs, F.A., and L.A. Simpson. 1981. Influence of flooding and soil moisture content on elongation of sugarcane in Trinidad. Expl. Agric. 17: 403-406.

Gyawali, S.R. 1986. Diet Analysis of Greater One Horned Rhinoceros (*Rhinoceros unicornis*) by Fecal Analysis. M.S. Thesis, Tribhuvan University, Kathmandu, Nepal. 34 pp + illus.

Hara, H., A.O. Chater, and L.H.J. Williams. 1978-1982. An Enumeration of the Flowering Plants of Nepal, 3 Volumes. British Museum (Natural History), London.

Heady, H. 1975. Rangeland Management. McGraw-Hill Book Company, New York. 460 pp.

Heady, H.F. 1957. The effect of cages on yield and composition in the California annual type. J. Range Manage. 10: 175.

Heinselman, M.L. 1981. Fire and succession in conifer forests of northern North America. Pages 374-405 in West, D.C., H.H. Shugart, and D.B. Botkin (eds.). Forest Succession: Concepts and Applications. Springer-Verlag, New York.

Hilbert, D.W., D.M. Swift, J.K. Detling , and M.I. Dyer. 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia 51: 14-18.

Hill, M.O. 1979a. TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way by classification of the individuals and attributes. Cornell University, Ithaca, New York.

Hill, M.O. 1979b. DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca,New York.

HMG. 1968. Soil Survey of Chitwan Division. Forest Resources Survey Publication No. 5. HMG Dept. Forests, Kathmandu, Nepal.

Holm, L.C. 1969. Weed problems in developing countries. Weed Sci. 17: 113-118.

Holm, L.C., D.L. Plucknett, J.V. Pancho, and J.P. Herberger. 1977. The World's Worst Weeds. University of Hawaii Press, Honolulu, Hawaii. 609 pp.

Hooker, J.D. 1872-97. Flora of British India. 7 vols. Reeve, London.

Hool, J.N. 1966. A dynamic programming-Markov chain approach to forest production control. For. Sci. Monog. 12: 1-26.

Horn, H.S. 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5: 25-37.

Horn, H.S. 1976. Succession. Pages 187-204 in May, R.M. (ed.). Theoretical Ecology. W.B. Saunders, Philadelphia.

Hubbard, C.E., R.O. Whyte, D. Brown, and A.P. Gray. 1944. *Imperata cylindrica*: taxonomy, distribution, and economic significance and control. Imperial Agricultural Bureau Joint Publication. Imperial Forestry Bureau Oxford, Oxford. 63pp.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69: 46-58.

Huntley, B.J., and B.H. Walker (eds.). 1982. Ecology of Tropical Savannas. Springer-Verlag, Berlin. 669 pp.

Hurlbert, S.H. 1984. Psuedoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211.

Huston, M., and T. Smith. 1987. Plant succession: life history and competition. Am. Nat. 130: 16-198.

Inglis, J. 1892. Tent Life in Tigerland and Sport and Work on the Nepaul Frontier. London.

Ivens, G.W. 1983. The natural control of *Imperata cylindrica* in Nigeria and northern Thailand. Mount. Res. and Develop. 3: 372-377.

James, S.W. 1988. The postfire environment and earthworm populations in tallgrass prairie. Ecology 69: 476-483.

Jameson, D.A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29: 532-594.

Jerdon, T. 1874. The Mammals of India. London. 335 pp.

Johnson, I.R., and A.J. Parsons. 1985. A theoretical analysis of grass growth under grazing. J. Theor. Biol. 112: 345-367.

Jones, C.A. 1985. C_4 Grasses and Cereals. Wiley, New York. 419 pp.

Juang, T.C., and G. Uehara. 1971. Effect of ground-water table and soil compaction on nutrient element uptake and growth of sugarcane. Int. Soc. Sugar Cane Technol. Proc. 14: 679-687.

Kakde, J.R. 1985. Sugarcane Production. Metropolitan Book Co., New Delhi. 384 pp.

Kanjilal, P.C. 1933. A Forest Flora for Pilibhit, Oudh, Gorakhpur and Bundelkhand. Narendra Publishing House, Delhi. 427 pp.

Kellman, M., K. Miyanishi, and P. Hiebert . 1985. Nutrient retention by savanna ecosystems: II. Retention after fire. J. Ecology 73: 953-962.

Klein, D.R. 1970. Food selection by North American deer and their response to over utilization of preferred plant species. Pages 25-46 in Watson, A. (ed.). Animal Populations in Relation to Their Food Resources. Blackwell Scientific, Oxford.

Knoop, W.T., and B.H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. J. Ecology 73: 235-253.

Kucera, C.L. 1981. Grasslands and fire. Pages 90-111 in Fire Regimes and Ecosystem Properties. USDA Forest Service Gen. Tech. Rep. WO-26. USDA Forest Service, Washington, D.C.

Kucera, C.L., and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology 43: 334-336.

Kushawa, S.P.S., P.S. Ramakhrishnan, and R.S. Tripathi. 1983. Competition between *Imperata cylindrica* and *Eupatorium odoratum* at 2 levels of nitrogen-phosphorus-potassium treatment. Proc. Indian Nat. Sci. Acad. Part B, Biol. Sci. 49: 50-56.

Lahiri, A.N., and B.C. Karabanda. 1964. Germination studies on arid zone plants. III. Some factors influencing the germination of grass seeds. Nat. Inst. Sci. India Proc. 30B: 186-196.

Lamotte, M., and F. Bourliere. 1983. Energy flow and nutrient cycling in tropical savannas. Pages 583-604 in Bourliere, F. (ed.). (*q.v.*).

Larcher, W. 1983. Physiological Plant Ecology. Springer-Verlag, Berlin. 303 pp.

Lauenroth, W.K., H.W. Hunt, D.M. Swift , and J.S. Singh. 1986. Estimating aboveground net primary production in grasslands: a simulation approach. Ecol. Modelling 33: 297-314.

Laurie, A. 1982. Behavioural ecology of the greater one-horned rhinoceros. J. Zool., Lond. 196: 307-341.

Laurie, W.A. 1979. The Ecology and Behaviour of the Greater One-horned Rhinoceros. Ph.D. Diss., University of Cambridge, Cambridge.

Lee, J.J., and D.L. Inman. 1975. The ecological role of consumers-an aggregated systems view. Ecology 56: 1455-1458.

Lehmkuhl, J.F., R.K. Upreti, and U.R. Sharma. 1988. National parks and local development: grasses and people in Royal Chitwan National Park, Nepal. Environ. Conserv. 15: 143-148.

Lemon, P.C. 1968. Fire and wildlife grazing on an African plateau. Proc. Tall Timbers Fire Ecol. Conf. 8: 71-88.

Lineham, P.A., J. Lowe, and R.H. Stewart. 1952. The output of pasture and its measurement. Part 3. J. Brit. Grassl. Soc. 7: 73-98.

Lippe, E., J.T. De Smidt, and D.C. Glenn-Lewin. 1985. Markov models and succession: a test from a heathland in the Netherlands. J. Ecology 73: 775- 791.

Lloyd, P.S. 1972. Effects of fire on a Derbyshire grassland community. Ecology 53: 915-920.

Loucks, O.L., M.L. Plumb-Mentjes, and D. Rogers. 1985. Gap processes and large-scale disturbances in sand prairies. Pages 72-85 in Pickett, S.T.A. and P.S. White (eds.). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida.

Lydekker, R. 1924. The Game Animals of India, Burma, Malaya, and Tibet. Ward, London.

Mack, R.N., and J.N. Thompson. 1984. Evolution in steppe with few large, hooved mammals. Am. Nat. 119: 757-773.

MacMahon, J.A. 1981. Successional processes: comparisons between biomes with special reference to probable roles of and influences on animals. Pages 277- 304 in West, D.C., H.H. Shugart, and D.B. Botkin (eds.). Forest Succession Concepts and Application. Springer-Verlag, New York.

Mathur, Y.K. 1984. Cenozoic palynofossils, vegetation, ecology and climate of the north and northwestern sub-Himalayan region, India. Pages 504-552 in Whyte, R.O. (ed.) (*q.v.*).

McAtee, J.W., C.J. Scifres, and D.L. Drawe. 1979. Digestible energy and protein content of Gulf cordgrass following burning and shredding. J. Range Manage. 32: 376-378.

McCormick, J. 1968. Succession. Student Publications, School of Fine Arts, Univ. of Penn. VIA1: 22-35, 121-132.

McKay, G.M., and J.F. Eisenberg. 1974. Movement patterns and habitat utilization of ungulates in Ceylon. Pages 708-721 in Geist, V. and F. Walther (eds.). The Behavior of Ungulates in Relation to Management, Vol. 2. IUCN, Morges, Switzerland.

McNaughton, S.J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191: 92-94.

McNaughton, S.J. 1979a. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113: 691-703.

McNaughton, S.J. 1979b. Grassland-herbivore dynamics. Pages 46-81 in Sinclair, A.R.E. and M. Norton-Griffiths (eds.). Serengeti: Dynamics of an Ecosystem. University of Chicago press, Chicago.

McNaughton, S.J. 1983. Serengeti grassland ecology: The role of composite environmental factors and contingency in community organization. Ecological Monographs 53: 291-320.

McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. Am. Nat. 124: 863-886.

McNaughton, S.J. 1985a. Ecology of a grazing ecosystem: the Serengeti. Ecol. Monogr. 55: 259-294.

McNaughton, S.J. 1985b. Interactive regulation of grass yield and chemical properties by defoliation, a salivary chemical, and inorganic nutrition. Oecologia 65: 478-486.

McNaughton, S.J. 1986a. On plants and herbivores. Am. Nat. 128: 765-770.

McNaughton, S.J., and F.S. Chapin. 1985. Effects of phosphorus nutrition and defoliation on C_4 graminoids from the Serengeti plains. Ecology 66: 1617-1629.

McNaughton, S.J., M.B. Coughenour, and L.L. Wallace. 1982. Interactive processes in grassland ecosystems. Pages 167-194 in Estes, J.R. et. al. (eds.) (*q.v.*).

Michelmore, A.P.G. 1939. Observations on tropical African grasslands. J. Ecology 27: 282-312.

Milford, R. 1957. The usefulness of lignin as an index of forage consumed by ruminants. Pages 79-85 in Lignification of Plants in Relation to Ruminant Nutrition. CSIRO, Canberra, Australia.

Milner, L., and R.E. Hughes. 1968. Methods for the Measurement of the Primary Production of Grassland. Blackwell Scientific, Oxford. 70 pp.

Milton, J., and G. Binney. 1980. Ecological planning in the Nepalese Terai. A report of conflicts between wildlife conservation and agriculture land use in Padampur Panchayat. Threshold Inc., Washington, D.C.

Mishra, H.R. 1982a. The Ecology and Behaviour of Chital (*Axis axis*) in the Royal Chitwan National Park, Nepal. Ph.D. Dissertation, University of Edinburgh. 240 pp.

Mishra, H.R. 1982b. Balancing human needs and conservation in Nepal's Royal Chitwan National Park. Ambio 6:246-257.

Mishra, H.R. 1984. A delicate balance: tigers, rhinoceros, tourists, and park management vs the needs of local people in Royal Chitwan National Park, Nepal. Pages 197-203 in McNeely, J.A. and K.R. Miller (eds.). National Parks, Conservation, and Development. Smithsonian Institution Press, Washington, D.C.

Mishra, H.R. and E. Dinerstein. 1987. New Zip Codes for resident rhinos in Nepal. Smithsonian, July: 67-73.

Misra, R. 1946. A study of the ecology of low-lying lands. Indian Ecol. 1: 27- 47.

Misra, R. 1979. Part IV. Tropical grasslands. Pages 188-244 in Coupland, R.T. (ed.). Grassland Ecosystems of the World: Analysis of Grasslands and Their Uses (IBP 18). Cambridge University Press, Cambridge.

Misra, R. 1983. Indian savannas. Pages 151-166 in Bourliere, F. (ed.) (*q.v.*).

Moore, A.W. 1960. The influence of annual burning on a soil in a derived savanna zone of Nigeria. Trans. Int. Congr. Soil Sci., Madison, Wisc. 4: 257-264.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York. 547 pp.

Mukherjee, A.K. 1982. Endangered Animals of India. Zoological Survey of India, Calcutta. 122 pp.

Noble, I.R., and R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5-21.

Noy-Meir, I. 1982. Stability of plant-herbivore models and possible applications to savanna. Pages 591-609 in Huntley, B.J. and B.H. Walker (eds.). Ecology of Tropical Savannas. Springer-Verlag, New York.

Noy-Mier, I. 1975. Stability of grazing systems: an application of predator- prey graphs. J. Ecology 63: 459-481.

Old, S.M. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecol. Monogr. 39: 355-384.

Oldfield, H.A. 1880. Sketches from Nepal, Historical and Descriptive. W.H. Allen, London.

Oliver, W.L.R. 1980. The Pygmy Hog: The Biology and Conservation of the Pygmy Hog and the Hispid Hare. Special Scientific Report No.1. The Jersey Wildlife Preserv. Trust, Jersey. 80 pp.

Owen-Smith, N., and P. Novellie. 1982. What should clever ungulate eat?. Am. Nat. 119: 151-178.

Peet, R.K., and N.L. Christensen. 1980. Succession: a population process. Vegetatio 43: 131-140.

Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. American Naturalist 110: 107-119.

Pickett, S.T.A., S.L. Collins, and J.J. Armesto. 1987. A hierarchical consideration of causes and mechanisms of succession. Vegetatio 69: 109-114.

Pickett, S.T.A., and P.S. White. 1985. Patch dynamics: a synthesis. Pages 371- 384 in Pickett, S.T.A. and P.S. White (eds.). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida.

Pitot, A., and H. Mason. 1951. Quelques donnees sur la temperature au cours des feux de brousse aux environs de Dakar. Bull. IFAN, A 13: 711-732.

Pollock, F., and W. Thom. 1900. Wild Sports of Burma and Assam. Hurst and Blackett, London.

Poore, M.E.D. 1962. The method of successive approximation in descriptive ecology. Adv. Ecol. Res. : 35-68.

Prater, S.H. 1971. Indian Animals, Third Edition. Bombay Natural History Society, Bombay. 324 pp.

Proceedings of the Symposium on Ecology of Animal Populations. 1982. Zoological Survey of India, Calcutta. 188 pp.

Puri, G.S. 1960. Indian Forest Ecology. Oxford Book and Stationary Co., New Delhi.

Puri, G.S., V.M. Meher-Homji, R.K. Gupta, and S. Puri. 1983. Forest Ecology (2nd Edition). Volume I. Phytogeography and Forest Conservation. Oxford & IBH Publishing Co., New Delhi. 549 pp.

Quinn, J.F., and A.E. Dunham. 1983. On hypothesis testing in ecology and evolution. Am. Nat. 122: 602-617.

Redetzke, K.A., and G.M. Van Dyne. 1976. A matrix model of a rangeland grazing system. J. Range Manage. 29: 425-430.

Redetzke, K.A., and G.M. Van Dyne. 1979. Data-based, empirical, dynamic matrix modeling of rangeland grazing systems. Pages 157-172 in French, N.R. (ed.). Perspectives in Grassland Ecology. Springer-Verlag, New York.

Robertson, G.P., M.A. Huston, F.C. Evans, and J.M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology 69: 1517-1524.

Rodgers, W.A. 1986. The role of fire in the management of wildlife habitats: a review. Indian Forester 112: 845-857.

Roy, S.D. 1986. Fire in wet grassland habitats of Assam. Indian Forester 112: 914-919.

Ruess, R.W., S.J. McNaughton, and M.B. Coughenour. 1983. The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an East African sedge. Oecologia 59: 253-261.

San Jose, J.J., and E. Medina. 1975. Effect of fire on organic matter production in a tropical savanna. Pages 251-264 in Golley, F.B. and E. Medina (eds.). Tropical Ecological Systems. Springer-Verlag, Berlin.

Sarmiento, G. 1983. The savannas of tropical america. Pages 245-288 in Bourliere, F. (ed.) (*q.v.*).

Saxena, K.G., and P.S. Ramakrishnan. 1983. Growth and allocation strategies of some perennial weeds of slash and burn agriculture (Juhm) in northwestern India. Can. J. Bot. 61: 1300-1306.

Schaller, G.B. 1967. The Deer and the Tiger: A Study of Wildlife in India. University of Chicago Press, Chicago. 370 pp.

Schmid, M. 1958. Flore agrostologique de l'Indochine. Agron. Trop. 13: 1-320.

Schmid, M. 1974. Vegetation du Vietnam. Le massif sud-Annamitique et les regions limitrophes. Mem. ORSTOM 74: 1-243.

Seastedt, T.R. 1985. Canopy interception of nitrogen in bulk precipitation by annually burned and unburned tallgrass prairie. Oecologia 66: 88-92.

Seidensticker, J. 1976. Ungulate populations in Chitwan Valley, Nepal. Biol. Conserv. 10: 183-210.

Sharma, U.R. 1986. A study of park-people interaction in Royal Chitwan National Park. Report submitted to World Wildlife Fund US. 29 pp.

Sharrow, S.H., and I. Motazedian. 1983. A comparison fo three methods for estimating forage disappearance. J. Range Manage. 36: 469-471.

Shugart, H.H., and D.L. Urban. 1986. Modeling habitat relationships of terrestrial vertebrates - a researcher's viewpoint. Pages 425-429 in Verner, J., M.L. Morrison, and C.J. Ralph (eds.). Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison.

Shugart, H.H.J.r., T.R. Crow, and J.M. Hett. 1973. Forest succession models: a rationale and methodology for modeling forest succession over large regions. Forest Science 19: 203-212.

Shugart, H.H.J.r., and D.C. West. 1980. Forest succession models. BioScience 30: 308-313.

Sinclair, A.R.E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. J. Anim. Ecol.: 497-520.

Singh, J.S., W.K. Lauenroth, and R.K. Steinhorst. 1975. Review and assessment of various techniques for estimating net aerial primary productivity in grassland from harvest. Bot. Review 41: 181-232.

Slobodkin, L.B., F.E. Smith, and N.G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. Am. Nat. 101: 109-124.

Smeins, F.E., and D.E. Olson. 1970. Species composition and production of a native northwestern Minnesota tall grass prairie. Am. Midl. Nat. 84: 398-410.

Smith, E.F., V.A. Young, K.L. Anderson, W.S. Rullifson, and S.N. Roger. 1960. The digestibility of forage on burned and unburned bluestem pasture as determined with grazing animals. J. Anim. Sci. 19: 388-391.

Smith, E.L. 1960. Effects of burning and clipping at various times during the wet season on tropical tall grass range in northern Australia. J. Range Manage. 13: 197-203.

Smith, J.L.D. 1984. Dispersal, communication, and conservation strategies for the tiger (*Panthera tigris*) in Royal Chitwan National Park, Nepal. Ph.D. Diss., University of Minnesota, Minneapolis.

Smythies, E. 1942. Big Game Shooting in Nepal. Thacker, Spink and Co., Calcutta.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. W.H. Freeman, New York. 859 pp.

Spillet, J.J., and K.M. Tamang. 1966. Wildlife conservation in Nepal. J. Bombay Nat. Hist. Soc. 63: 573-575.

Stebbins, G.L. 1981. Coevolution of grasses and herbivores. Ann. Missouri Bot. Gard. 68: 75-86.

Stewart, J.L., and D. Brandis. 1874. The Forest Flora of North-West and Central India. 2 vols. Allen, London. 608 pp.

Stroud, D.O., R.H. Hart, M.J. Samuel , and J.D. Rodgers . 1985. Western wheatgrass responses to simulated grazing. J. Range Manage. 38: 103- 108.

Sunquist, M.E. 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. Smithsonian Contri. to Zool. No. 3.

Swartzman, G.L., and S.P. Kaluzny. 1987. Ecological Simulation Primer. MacMillan, New York. 370 pp.

Swartzman, G.L., and J.S. Singh. 1974. A dynamic programming approach to optimal grazing strategies using a succession model for a tropical grassland. J. Appl. Ecol. 11: 537-548.

t'Mannetje, L. 1978. Measuring quantity of grassland vegetation. Pages 63-95 in t'Mannetje, L. (ed.). Measurement of Grassland Vegetation and Animal Nutrition. Commonwealth Agr. Bureau, Hurley, England.

Tabachnick, B.G., and L.S. Fidell. 1983. Using Multivariate Statistics. Harper and Row, New York. 509 pp.

Talbot, L.M. 1959. A look at threatened species. Oryx 5: 153-293.

Tamang, K.M. 1982. The status of the tiger (*Panthera tigris*) and its impact on principal prey populations in the Royal Chitwan National Park, Nepal. Ph.D. Diss., Michigan State University, Ann Arbor.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125: 827-852.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Monographs in Population Biology No. 26, Princeton University Press, Princeton, New Jersey. 360 pp.

Tinley, K.L. 1982. The influence of soil moisture balance on ecosystem patterns in southern Africa. Pages 175-192 in Huntley, B.J. and B.H. Walker (eds.) (*q.v.*).

Toole, V.K. 1973. Effects of light, temperature, and their interactions on the germination of seeds. Seed Sci. Technol. 1: 339-396.

Troth, R.G. 1976. Smithsonian plant ecology study working plan. Mimeo report submitted to the HMG Department of National Parks and Wildlife Conservation, Kathmandu, Nepal. 20 pp.

Troth, R.G., and D.H. Nicolson. 1977. Artificial key to the common shrubs of the riverine forests, Royal Chitwan National Park, Nepal. Phytologia 35: 224-228.

Usher, M.B. 1981. Modelling ecological succession, with particular reference to Markovian models. Vegetatio 46: 11-18.

van der Hammen, T. 1983. The paleoecology and paleogeography of savannas. Pages 19-35 in Bourliere, F. (ed.) (*q.v.*).

Van Soest, P.J. 1982. Nutritional Ecology of the Ruminant. O & B Books, Inc., Corvallis, Oregon. 374 pp.

Van Hulst, R. 1978. On the dynamics of vegetation: patterns of environmental and vegetation change. Vegetatio 38: 65-75.

Van Hulst, R. 1979. On the dynamics of vegetation: Markov chains as models of succession. Vegetatio 40: 3-14.

Van Dyne, G.M., N.R. Brockington, Z. Szocs, J. Duek, and C.A. Ribic. 1980. Large herbivore subsystem. Pages 269-537 in Breymeyer, A.I. and G.M. Van Dyne (eds.). Grasslands, Systems Analysis, and Man. IBP 19. Cambridge University Press, Cambridge.

Villecourt, P., W. Schmidt, and J. Cesar. 1979. Recherche sur le composition chimique (N, P, K) de la strate herbacee de la savane de Lamto (Cote de Ivoir). Rev. Ecol. Biol. Sol. 16: 9-15.

Vishnu-Mittre. 1984. Floristic change in the Himalaya (southern slopes) and Siwaliks from the mid-Tertiary to recent times. Pages 483-503 in Whyte, R.O. (ed.) (*q.v.*).

Vogle, R.J. 1974. Effects of fire on grasslands. Pages 139-194 in Kozlowski, T.T. and C.E. Ahlgren (eds.). Fire and Ecosystems. Academic Press, New York.

Voigt, P.W. 1973. Induced seed dormancy in weeping lovegrass, *Eragrostis curvula.* Crop Science 13: 76-79.

Wadia, D.N. 1953. Geology of India. MacMillan, London. 531 pp.

Waksman, S.A. 1927. Principles of Soil Microbiology. Williams and Wilkins, Baltimore. 897 pp.

Walker, B.H., D. Ludwig, C.S. Holling, and R.M. Peterman. 1981. Stability of semi-arid savanna grazing systems. J. Ecology 69: 473-498.

Wallace, L.L. 1987. Effects of clipping and soil compaction on growth morphology and mycorrhizal colonization of *Schizachyrium scoparium*, a C_4 bunchgrass. Oecologia 72: 423-428.

Weaver, J.E., and N.W. Rowlands. 1952. Effects of excessive natural mulch on development, yield, and structure of native grassland. Bot. Gaz. 114: 1-19.

Weinstein, D.A., and H.H. Shugart. 1983. Ecological modeling of landscape dynamics. Pages 29-45 in Mooney, H. and M. Gordon (eds.). Disturbance & Ecosystems. Springer-Verlag, New York.

Werner, P.A. 1976. Ecology of plant populations in successional environments. Syst. Bot. 1: 246-268.

West, R.M. 1984. Siwalik faunas of Nepal: paleoecologic and paleoclimatic implications. Pages 724-744 in Whyte, R.O. (ed.) (*q.v.*).

Wharton, C. 1968. Man, fire and wild cattle in southeast Asia. Proc. Tall Timbers Fire Ecol. Conf. 8: 107-167.

White, P.S., and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-16 in Pickett, S.T.A. and P.S. White (eds.). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Whyte, R.O. 1957. The Grassland and Fodder Resources of India. Indian Council of Agr. Res. Sci. Monogr. 22. 437 pp.

Whyte, R.O. (ed.). 1984. Evolution of the East Asian Environment. Vol. II. Paleobotany, Paleozoology, and Paleoanthropology. University of Hong Kong, Hong Kong.

Wiegert, R.G. 1962. The selection of an optimum quadrat size for sampling the standing biomass of grasses and forbs. Ecology 43: 125-129.

Wiegert, R.G., and F.C. Evans. 1967. Investigation of secondary productivity of grasslands. Pages 499-516 in Petruzewicz, K. (ed.). Secondary Productivity of Ecosystems. Polish Academy of Science, Warsaw-Krakow.

Wright, H.A., and A.W. Bailey. 1982. Fire Ecology. Wiley and Sons, New York. 501 pp.

Yadava, P.S., and J.S. Singh. 1977. Grassland Vegetation: It's Structure, Function, Utilization, and Management. Today & Tomorrow's Publishers, New Delhi. 182 pp.

Younger, V.B. 1972. Physiology of defoliation and regrowth. Pages 292-303 in Younger, V.B. and C.M. McKell (eds.). The Biology and Utilization of Grasses. Academic Press, New York.

VITA

Name: John F. Lehmkuhl

Education:

Mater Dei High School
Santa Ana, California

California State University
Fullerton, California

Humboldt State University
Arcata, California
B.S. Wildlife Biology, 1974

University of Montana
Missoula, Montana
M.S. Wildlife Ecology, 1981

University of Washington
Seattle, Washington
Ph.D. Forest Resources, 1989