AN ECOLOGICAL SURVEY OF THE ROYAL KARNALI-BARDIA WILDLIFE RESERVE, NEPAL. PART I: VEGETATION, MODIFYING FACTORS, AND SUCCESSIONAL RELATIONSHIPS

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ABSTRACT

The vegetation of a newly created tiger sanctuary in south-western Nepal is described in detail. Six major vegetational associations were identified. It was found that several subtypes of Shorea robusta *forest covered over* 70% *of the land area of the reserve. Open grassland, savannah, and riverine forest accounted for the rest. Modifying factors which have altered vegetational composition and wildlife habitat are discussed. The most serious of these influences have been man's activities in relation to clearing for cultivation, grazing of domestic stock, and uncontrolled burning. A model of successional patterns observed within the Karnali-Bardia Wildlife Reserve is proposed.*

INTRODUCTION

While research projects investigating the ecology of a number of endangered wildlife species of the Nepalese Terai have begun, their major focus has been restricted to population studies. Quantification of the habitat types utilised by the tiger *Panthera tigris*, the swamp deer *Cervus duvauceli*, and the one-horned rhinoceros *Rhinoceros unicornis* through vegetational analysis has not proceeded with equal intensity. Results from habitat utilisation research in Karnali-Bardia (this study), Chitawan National Park, Nepal (Seidensticker, 1976), and in other sanctuaries of South Asia (Eisenberg & Seidensticker, 1976) indicate that some of the most valuable wildlife habitats in these areas are in early to mid-successional stages of development.

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Without a better understanding of the successional relationships which exist between flood plain, savannah, and forest associations, wildlife managers will be hard pressed in the future to determine how long-term changes in the vegetational composition and profile will affect overall habitat utilisation. The major effort of this paper, then, is to provide baseline data which may prove useful in describing the complexities of the interactions between the vegetation and the wildlife of the Terai and ultimately in development of habitat management plans for the conservation of its endangered fauna.

DESCRIPTION OF THE STUDY AREA

The Royal Karnali-Bardia Wildlife Reserve is located in the southwestern corner of Nepal at 81°20'E, 28°35'N (Fig. 1). Originally established as a Royal hunting reserve, Karnali-Bardia was reclassified as a wildlife sanctuary and officially gazetted as such in 1976. The few historical records which do exist indicate that Karnali-Bardia was seldom used for Royal outings. Human encroachment on the habitat of a number of important and endangered wildlife species, however, has been well documented (Mishra, 1974). A grassland area, known as Baghora Phanta, was under cultivation only a decade ago. The grazing of domestic stock within the reserve remained uncontrolled until 1975. The cutting of firewood and building timber, the gathering of forest products, and poaching also continued essentially unhindered until then. In spite of these undesirable factors, one area of Karnali-Bardia, the south-western corner, still supported high densities of wild ungulates. In addition, this same section was characterised by a wide diversity of habitat types over a relatively small area. One of the primary objectives of this study was to measure the relationship between habitat diversity and wild ungulate biomass. An intensive study site in the south-western corner of the reserve was deemed the most appropriate location to investigate this subject, as well as other research priorities.

The climate of the reserve, like much of South Asia, is typically monsoonal with most of the annual precipitation occurring during four months of the year (Fig. 2). Although the actual monsoon season in Karnali-Bardia may not begin until late June, heavy premonsoon showers in April and May are quite common, as they were in 1977. The monsoon period usually ends by early October. As the monsoon originates in the Bay of Bengal and arrives from the southeast, it has been found that the western Terai usually receives less rainfall and the monsoon period itself lasts for a shorter duration than in the eastern Terai. The rainfall data from Chisapani (located along the Karnali River at the base of the first range of the Himalayan foothills) and from Gularia (in a treeless agricultural area several kilometres from a major water source) probably represent the upper and lower limits, respectively, of the rainfall variation found within the reserve. Most of Karnali-Bardia probably receives an amount that falls between the two.

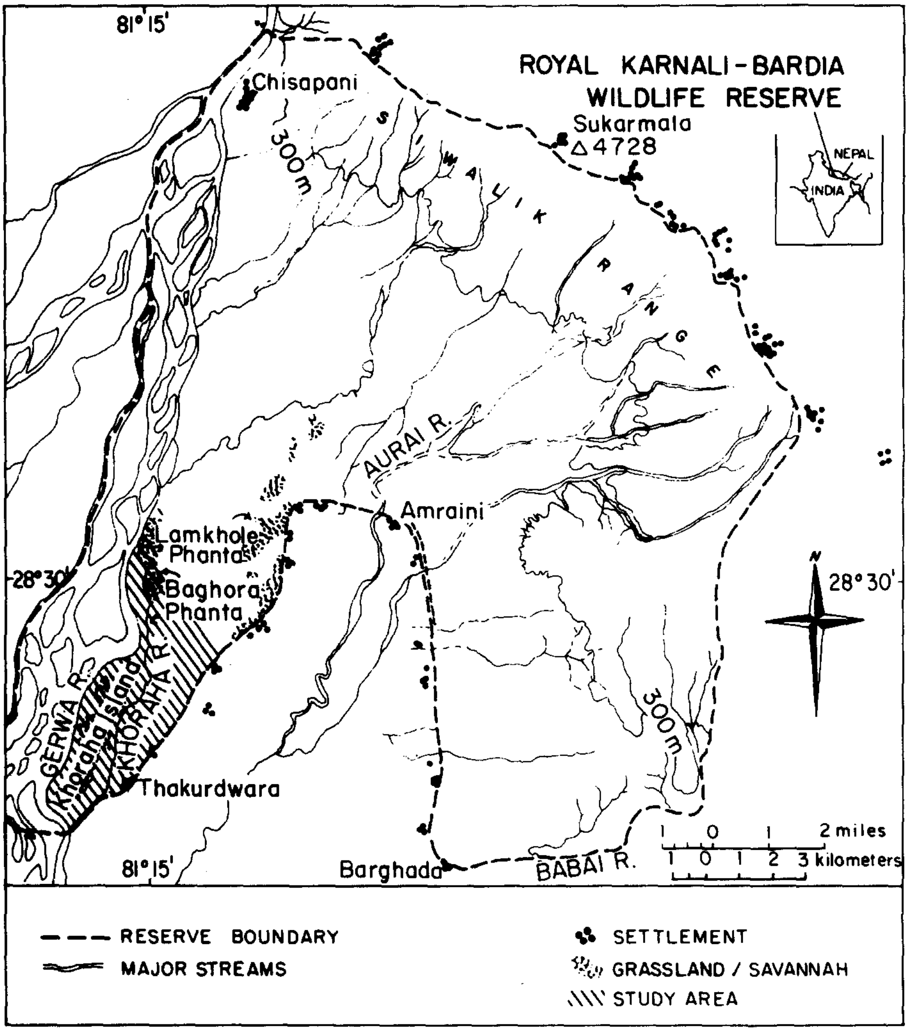

Fig. 1. Bordered on the north by the outermost range of the Himalayas, the Royal Karnali-Bardia Wildlife Reserve is one of four newly created wildlife sanctuaries in the Nepalese Terai. The primary purpose behind its establishment is to protect one of the largest remaining tiger populations of this region.

Temperature data recorded at Chisapani over a seven-year period are presented in Fig. 3. Three distinct seasons exist in the Terai. Following the monsoon is a cool period lasting from November until mid-February. The lowest temperatures of the year occur in December and January. Temperatures increase steadily during the hot season (mid-February to June) until the annual maximum is reached in May.

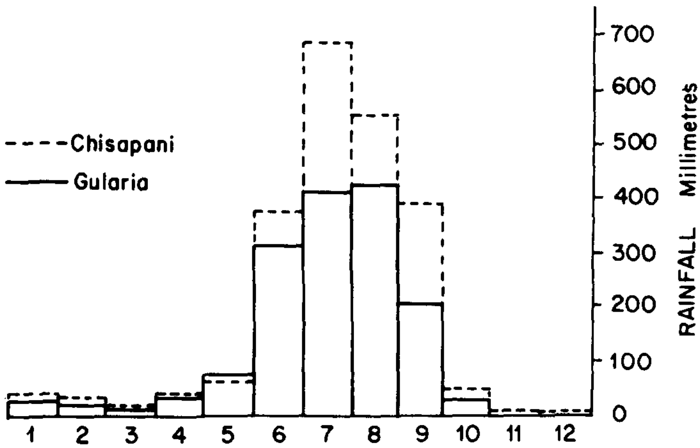

Fig. 2. Average annual rainfall 1968–72 recorded at Chisapani and Gularia (from Bolton, 1976).

Relative humidity, which remains low throughout most of the hot season, increases with the onset of the pre-monsoon rains.

An altitudinal gradient prevails over Karnali-Bardia's 348 km^2. The northern border of the reserve is formed by the crest of the Churia (Siwalik) ridge and reaches an elevation of 1441 m at Sukarmala. The southern section, however, is characteristic of the low-lying unbroken terrain of the Terai. The study area, located in the southwestern corner of the reserve, lies at an elevation of 152 m above sea level.

The Siwalik or Churia range is composed of late Tertiary material. This formation contains fine-grained sandstone with deposits of clay, shale, freshwater limestone, and conglomerate. Soils of the south-facing Churia slopes are shallow and easily subject to erosion. Landslides occurred several times during the monsoon months between 1975 and 1977. The broad alluvial plain that slopes gently away from the base of the Churias to India is known as the bhaber. Most of the land area of Karnali-Bardia fits into this category. Bhaber deposits are composed of boulders, cobbles, and coarse sand layers amidst silt and clay (His Majesty's Government, Nepal, Soil Survey of Bardia Division, 1971). The bhaber soils are well drained and relatively deep. The study area itself is predominantly underlain by sandy loams. Soils of the flood plain islands in the Gerwa River and along its banks range from sands to gravels to sandy loams.

The reserve is bordered on the west by the Gerwa River and on the East by the Babai River, both of which provide a year-round source of water. Annually, the Gerwa and the Babai deposit large amounts of silt on their flood plains and along their banks. The Aurai River, which flows through the centre of the reserve, is also a perennial source of water. The small streams that drain the south-facing slopes of the Churia ridge are intermittent, holding water only during the monsoon period. The study area itself is one of the most well-watered sections of the reserve, being

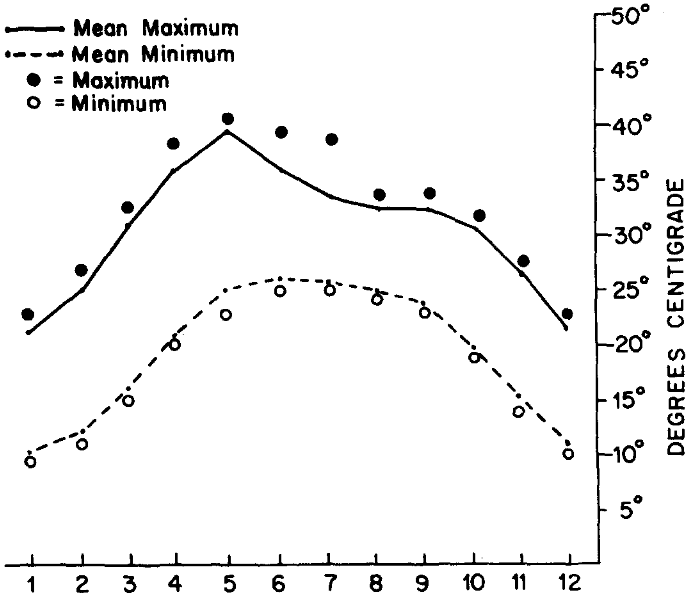

Fig. 3. Temperatures recorded at Chisapani 1965–1972 (adapted from Bolton, 1976).

bordered on the west by the Gerwa and on the east by a branch of the Gerwa known as the Khoraha. Four years ago the Khoraha was only an irrigation canal but with increased flow and erosion of its banks it has become a minor tributary.

METHODS

Vegetational analysis was carried out in four different plant associations (flood plain vegetation was sampled previously in Chitawan National Park, also located in the Terai). Since the associations differed widely in physiognomy (e.g. grassland as compared with *Shorea robusta-Buchanania latifolia* forest) and in distribution (e.g. *Bombax* savannah as compared with the *Ficus glomerata-Mallotus philippinensis-Eugenia jambolana* association), several different methods had to be employed.

For *Shorea robusta-Buchanania latifolia* forest and for the *Dalbergia sissoo-Acacia catechu* association a variation of Daubenmire's 15 × 25 m plot method was utilised (Fonda, 1974). In this method all trees over 2·5 cm diameter breast height falling within the plot are measured and the number of each species is recorded. The shrub layer (all plants over 1 m in height) was sampled by locating eight circular plots (demarcated by the length of the researcher's arm span) on four perpendicular lines traversing the 25 m long plot at 5, 10, 15, and 20 m. Whenever a species fell inside the demarcated circle a percent cover value was assigned to it. Low vegetation (all plants under 1 m in height) was measured with the use of 20 × 50 cm frames. Frames were placed systematically, 5 to a row, at 5, 10, 15, and 20 m. Estimates of bare ground were also included in the tally of percent cover of the low vegetation.

In three of the sampled forest associations, a 121.2 m × 7·5 m strip (Richards, 1952) was laid out. Within the strip all trees over 2·5 cm diameter breast height were measured. Using an Abney level, the total height of each tree, height to the first major branch, and the height of the lower limit of the crown were determined. Crown diameter was also recorded. Since tree crowns sometimes took irregular shapes, crown diameters were always measured on the same axis (aligned with the aid of a compass) to ensure continuity in sampling. From these data profile maps were drawn to scale for each of the three associations.

For the *Ficus glomerata–Mallotus philippinensis–Eugenia jambolana* forest a slight variation was used in order to compensate for the riparian distribution of this association. Instead of locating plots by completely random methods, they were laid contiguously along the banks of the Khoraha River and then back along one of the numerous ravines that extended down to the river bank from the interior of the island.

Tree species in the three forested habitats sampled were ranked by Importance Values. This figure was obtained by the summation of the relative frequency, relative density, and relative dominance for each species. Relative dominance was expressed as follows:

$$\frac{\text{total basal area of the species}}{\text{total basal area of all species}} \times 100$$

For the understory and low vegetation, ranking was achieved by the use of Prominence Values. This figure was computed by multiplying the percent cover value for each species by the square root of its frequency.

In the grassland habitats, cover and frequency values were obtained by using the point drop method (Phillips, 1959). Sampling was performed only during the monsoon period when almost all of the species encountered in this habitat were in flower.

The descriptions of the major vegetation types in Karnali-Bardia conform in general to the classifications of Champion & Seth (1968) for the North Indian Moist Deciduous Forest subtype. Once these associations were identified, their distributions over the 11·8 km^2 study area were mapped with the aid of aerial photographs. Interfaces between all associations were verified on the ground.

Nomenclature for plants follows Hooker (1872–97), Bor (1960), and Gupta (1969).

RESULTS AND DISCUSSION

Vegetative cover by habitat type is presented in Fig. 4. A total of six major habitat

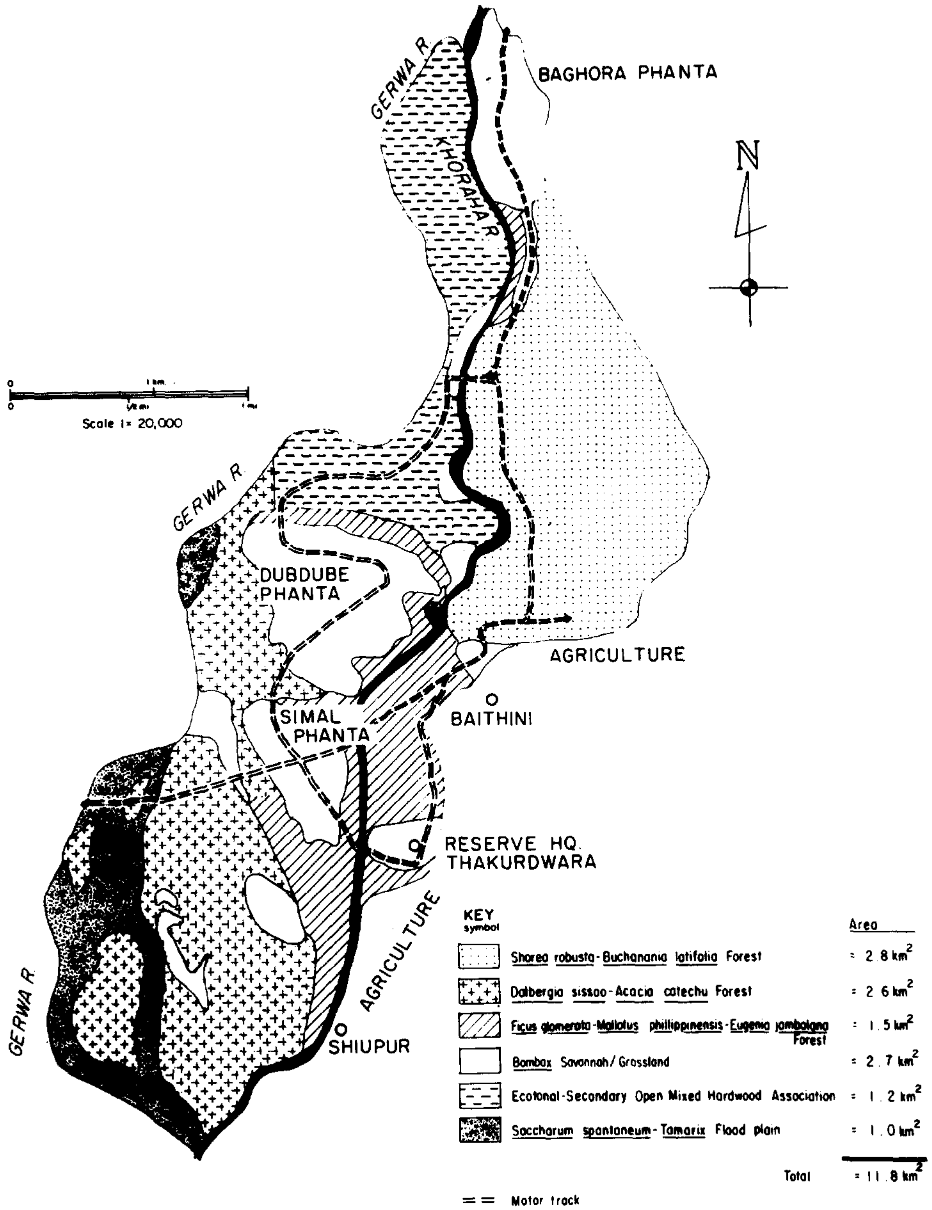

Fig. 4. Six major vegetational associations were identified within the study area. Part of the eastern and southern borders lay adjacent to cultivated fields and settlements.

types were identified within the study area. Their distribution, composition, and physiognomy are discussed below.

One of the most common associations encountered in the reserve is the *Shorea robusta-Buchanania latifolia* forest. *Shorea robusta* (or 'sal' as it is known generically) has been studied in great detail in India since it occupies a central role in the ecology of the forests of the subcontinent (Puri, 1960; Champion & Seth, 1968). This moist deciduous forest contains two canopy layers: the discontinuous upper canopy is dominated by *Shorea robusta* and *Terminalia tomentosa* while the lower canopy is composed of a number of smaller tree species (Fig. 5). The trees in the upper canopy may reach a height of 37 m while the lower layer averages about 10 m. It is important to remember that the profile maps of the different associations presented in Figs. 5, 6, and 7 represent only a 7·5 m slice of the forest. Such a long narrow strip sometimes gives the impression that the association resembles a savannah woodland rather than a true forest. Table 1 lists the different tree species encountered according to their importance values. The phenology of the dominant species in this and in the five other habitat types encountered is to be described elsewhere (Dinerstein in press).

The understory layer is composed primarily of *Shorea* seedlings and small *Buchanania* trees (Table 2). *Leea robusta*, a shrub, was leafless during the period of sampling, but during the monsoon becomes a conspicuous part of the understory. It is interesting to note that plant species designated by Srivastava (1965) as indicators of good and poor sal regeneration are both present in the same association. The low vegetation was poorly represented as the percent cover of bare ground indicates (Table 3). This also was attributable to sampling during the hot season. Once the pre-monsoon rains begin, a new growth of *Cyperus* sp., short grasses, and forbs cover the forest floor.

Visibility in this habitat type remains poor for most of the year, at times being restricted to less than 10 m. Only during the hot season when the annual fires burn out part of the understory vegetation does visibility improve substantially.

The above type of sal forest could be distinguished from two other subtypes found within the reserve. The differences in composition and physiognomy appeared to be a result of changes in topography, drainage, and soil conditions. Dry sal forest is characteristic of soils with a higher clay content on flat terrain. *Terminalia tomentosa*, *Shorea robusta*, and *Anogeissus latifolia* dominate the upper canopy layer. The understory, however, is composed primarily of tall and intermediate-sized grasses such as *Thysanolaena maxima*, *Erianthus ravennae*, *Apluda mutica*, and *Themeda* sp.

The third subtype, hill sal forest, occurs along the southern flanks of the Churia ridge. Perhaps because of the excessive drainage or low fertility of the soil found in this area the upper canopy trees do not reach the heights that they attain elsewhere in the reserve. Several other tree species often become more abundant than sal in this situation. *Phoenix acaulis*, a palm, is most conspicuous in the understory of this

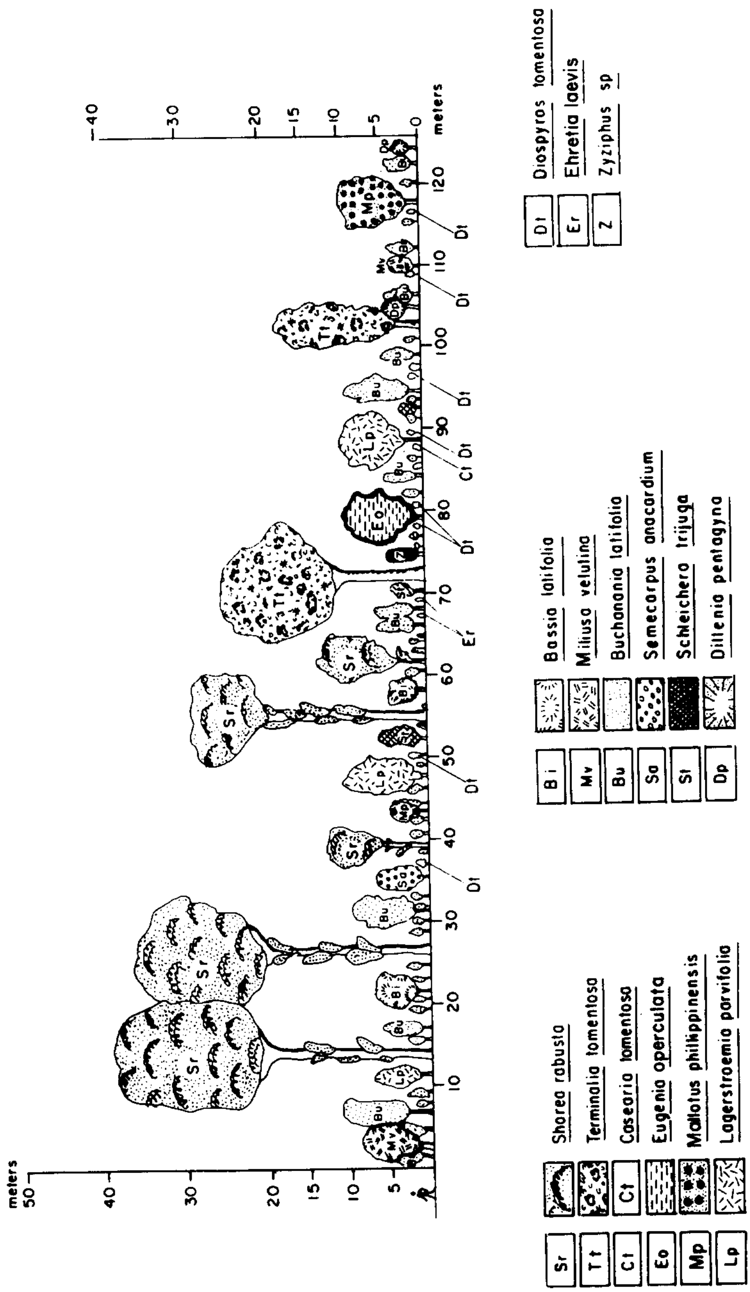

Fig. 5. Profile of a typical stand in the *Shorea robusta-Buchanania latifolia* forest from a 121 m × 7·5 m strip.

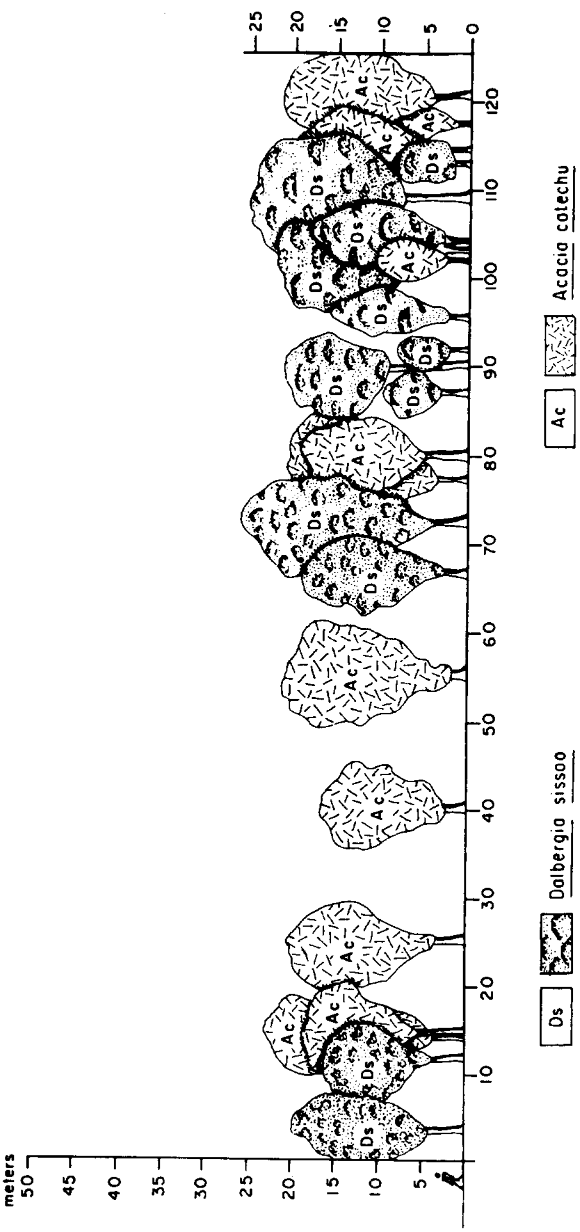

Fig. 6. Profile of a typical stand in the *Dalbergia sissoo-Acacia catechu* forest from a 121 m × 7·5 m strip.

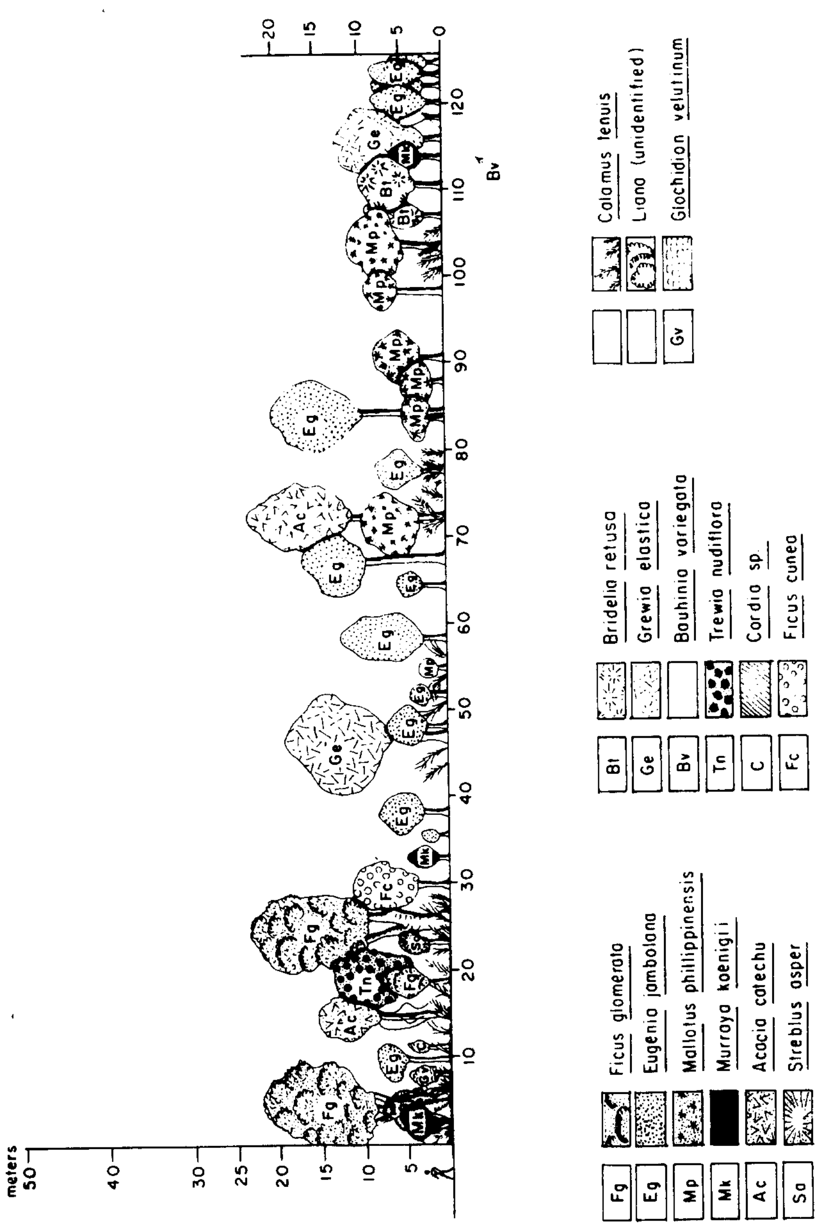

Fig. 7. Profile of a typical stand in the *Ficus glomerata-Mallotus phillippinensis-Eugenia jambolana* forest from a 121 m × 7·5 m strip.

TABLE 1
ANALYSIS OF THE TREE LAYER IN *Shorea robusta-Buchanania latifolia* FOREST

Species	*Relative density*	*Relative frequency*	*Relative dominance*	*Importance value*
Shorea robusta	19·1	10·5	60·1	89·7
Buchanania latifolia	36·1	10·5	2·5	49·1
Terminalia tomentosa	3·3	8·1	14·6	26·0
Miliusa velutina	7·2	7·0	0·8	15·0
Lagerstroemia parviflora	4·3	9·3	0·6	14·2
Mallotus phillippinensis	5·4	5·8	1·1	12·3
Dillenia pentagyna	3·6	8·1	0·6	12·3
Ficus benghalensis	0·4	1·2	10·3	11·9
Eugenia operculata	2·8	5·8	1·8	10·4
Ehretia laevis	3·6	5·8	0·2	9·6
Bassia latifolia	3·3	2·3	2·0	7·6
Semecarpus anacardium	2·9	3·5	0·3	6·7
Anogeissus latifolia	1·1	3·5	1·3	5·9
Spathalobus roxburghii	1·1	2·3	0·9	4·3
Zyziphus sp.	0·7	2·3	0·0	3·0
Unidentified	0·7	2·3	0·0	3·0
Litsea polyantha	0·7	2·3	0·0	3·0
Ficus rumphii	0·7	1·1	1·1	2·9
Schleichera trijuga	0·4	1·1	0·7	2·2
Oegenia dalbergiodes	0·7	1·1	0·2	2·0
Ficus cunia	0·4	1·1	0·5	2·0
Randia dumetorum	0·4	1·1	0·1	1·6
Eugenia jambolana	0·4	1·1	0·1	1·6
Bauhinia malabarica	0·4	1·1	0·0	1·5
Casearia tomentosa	0·4	1·1	0·0	1·5

Sample area = 0·1 ha.
No. of tree species in sample area = 25
Species density (species/0·1 ha) = 25
Stand density (trees/0·1 ha) = 277

subtype. Stainton (1972) described a similar type of forest in western Nepal. Although these latter two subtypes cover a large part of the reserve neither one is found within the study area.

Why does *Shorea robusta* compose such a large percentage of the forest cover in the Nepalese Terai and in India? One theory cites the cumulative effects of uncontrolled burning practices which favour sal, a fire-resistant species. Apart from anthropogenic influences, it has been established that seed predators and herbivores may severely limit the reproductive potential and distribution of certain plant species. In response to these pressures secondary compounds may have evolved through natural selection as a means to reduce the palatability of leaf tissue and seeds (Janzen, 1969, 1970, 1974*a*; Feeny, 1970). Quite a few plants in Karnali-Bardia are known to produce toxic alkaloids and phenolic compounds. *Shorea robusta* seeds contain a high concentration of tannins. Janzen (1974*b*) hypothesised that those dipterocarp species which fruit annually (as does sal), and occur where a number of potential seed predators are found, would possess toxic seeds. This second factor may help to explain the dominance of this species in some of the forest associations of the subcontinent.

TABLE 2
ANALYSIS OF THE UNDERSTORY IN *Shorea robusta-Buchanania latifolia* FOREST

Species	*% Cover*	*Frequency*	*Prominence value*
Buchanania latifolia	5·2	18	22·1
Shorea robusta	1·7	6	4·2
Ehretia laevis	1·1	8	3·1
Mallotus phillippinensis	1·1	4	2·2
Lagerstroemia parviflora	1·2	3	2·1
Diospyros tomentosa	0·5	3	0·9
Miliusa velutina	0·3	1	0·3
Bassia latifolia	0·1	1	0·1
Phoenix acaulis	0·1	1	0·1
Thespesia lampas	0·1	1	0·1
Indigofera pulchella	0·1	1	0·1

TABLE 3
ANALYSIS OF THE LOW VEGETATION IN THE *Shorea robusta-Buchanania latifolia* FOREST

Species	*% Cover*	*Frequency*	*Prominence value*
Bare ground	93·5	100	930·5
Shorea robusta	5·7	27	29·6
Moghania bracteata	4·2	23	20·1
Buchanania latifolia	2·9	4	5·8
Imperata cylindrica	1·0	14	3·7
Leea robusta	0·6	11	2·0
Diospyros tomentosa	1·1	3	1·9
Clerodendron infortunatum	0·8	3	1·4
Moghania sp.	0·4	4	0·8
Phoenix acaulis	0·3	4	0·6
Bassia latifolia	0·4	1	0·4
Ehretia laevis	0·4	1	0·4
Indigofera pulchella	0·2	2	0·3
Erianthus ravennae	0·1	1	0·1
Schleichera trijuga	0·1	1	0·1
Vetiveria zyzanoides	0·1	1	0·1

Another important association is the *Dalbergia sissoo-Acacia catechu* forest, commonly referred to as Khair-Sissoo forest. These two species have long been known to form the first seral stand of trees along the major river courses of the Terai because they are able to withstand flooding. Within the reserve this association is prevalent along the banks of the Gerwa River and on the islands within its flood plain (see Fig. 1). On these islands, stands of *Dalbergia sissoo* and *Acacia catechu* may occur either separately or together in combinations of varying proportions. Within the study area *Bombax ceiba* and *Streblus asper* were also mixed in with the first two species (Table 4). Puri (1960) associated the presence of species other than *D. sissoo* and *A. catechu* with changes in soil type.

Neither the understory layer (Table 5) nor the low vegetation (Table 6) were very prominent, probably because of the combined effects of grass cutting, the dormancy of a number of species during the hot season, and fire. Where heavy grazing by domestic stock has previously occurred, *Zyziphus mauritiana* and *Cassia tora*

TABLE 4

ANALYSIS OF THE TREE LAYER IN *Dalbergia sissoo-Acacia catechu* FOREST

Species	*Relative density*	*Relative frequency*	*Relative dominance*	*Importance value*
Dalbergia sissoo	50·4	35·2	58·2	143·8
Acacia catechu	39·5	35·2	38·9	113·6
Holoptelia integrifolia	7·5	5·9	1·3	14·7
Bombax ceiba	0·8	5·9	1·5	8·2
Ficus hispida	0·8	5·9	0·3	7·0
Streblus asper	0·8	5·9	0·1	6·8
Casearia tomentosa	0·8	5·9	0·1	6·8

Sample area = 0·1 ha
No. of tree species in sample area = 6
Species density (species/0·1 ha) = 6
Stand density (trees/0·1 ha) = 119

TABLE 5

ANALYSIS OF THE UNDERSTORY IN *Dalbergia sissoo-Acacia catechu* FOREST

Species	*% Cover*	*Frequency*	*Prominence value*
Aegeratum conyzoides	9·0	32	50·9
Colebrookia oppositifolia	8·5	27	44·2
Murraya koenigii	6·3	17	26·0
Pogostemon plectranthoides	4·8	25	24·0
Cassia tora	2·8	8	7·9
Erianthus ravennae	0·8	3	1·4

TABLE 6

ANALYSIS OF THE LOW VEGETATION IN *Dalbergia sissoo-Acacia catechu* FOREST

Species	*% Cover*	*Frequency*	*Prominence value*
Bare ground	32·0	47	224·0
Imperata cylindrica	30·0	43	196·7
Desmostachia bipinnata	17·3	27	89·9
Aegeratum conyzoides	9·0	22	42·2
Erianthus ravennae	5·3	10	16·8
Pogostemon plectranthoides	2·1	11	7·0
Vetiveria zyzanoides	1·5	3	2·6
Cynodon dactylon	1·1	4	2·2
Cassia tora	0·7	3	1·2
Zyziphus mauritiana	0·2	2	0·3
Colebrookia oppositifolia	0·1	1	0·1

become the most prominent species in the understory. During the monsoon a lush grass layer of *Imperata cylindrica*, *Vetiveria zyzanoides*, *Erianthus ravennae*, *Cynodon dactylon*, and *Cymbogon* sp. emerges.

The profile map of this association (Fig. 6) indicates the presence of only a single canopy layer. Individual trees in this habitat seldom reach above 25 m in height. Stand density varies considerably depending upon age, past burning histories, and soil conditions. As in *Shorea robusta* forest, visibility remains poor until the annual fires burn out the understory vegetation in April.

The third association, the *Ficus glomerata-Mallotus philippinensis-Eugenia jambolana* forest, closely resembles what Champion & Seth (1968) have called a 'West Gangetic Moist Mixed Deciduous Forest'. Buttressing is common among several of the tree species (e.g. *Bombax ceiba*, *Ficus glomerata*, and *Eugenia jambolana*). This may be a response to the boggy soil conditions which often prevail. The profile map (Fig. 7) reveals two canopy layers; the upper layer is dominated by *Ficus glomerata* and *Eugenia jambolana* while the lower layer is composed primarily of *Mallotus philippinensis* and young *Eugenia* trees. The upper canopy trees seldom exceed 25 m in height but most have wide spreading crowns which make them appear much larger. In the lower canopy most trees do not exceed 12 m. Eight tree species are relatively common to this type of forest (Table 7).

TABLE 7
ANALYSIS OF THE TREE LAYER IN *Ficus glomerata-Mallotus phillippinensis-Eugenia jambolana* FOREST

Species	*Relative density*	*Relative frequency*	*Relative dominance*	*Importance value*
Mallotus phillippinensis	32·4	13·3	22·3	68·0
Ficus glomerata	4·9	8·9	35·7	49·5
Eugenia jambolana	18·6	13·3	12·4	44·3
Murraya koenigii	8·8	13·3	0·9	23·0
Acacia catechu	2·9	6·7	10·3	19·9
Unidentified	9·8	6·7	2·6	19·2
Streblus asper	3·9	6·7	7·8	18·5
Grewia elastica	2·9	6·7	1·5	11·1
Ficus cunia	2·0	4·5	1·1	7·6
Casearia tomentosa	2·0	4·5	1·0	7·5
Litsea polyantha	2·0	4·5	0·6	7·1
Bridelia retusa	2·0	2·2	2·1	6·3
Cordia sp.	2·0	2·2	0·4	4·6
Trewia nudiflora	1·0	2·2	0·7	3·9
Ficus hispida	1·0	2·2	0·2	3·4
Bauhinia variegata	1·0	2·2	0·1	3·3

Sample area = 0·24 ha
No. of tree species in sample area = 16
Species density (species/0·1 ha) = 6·7
Stand density (trees/0·1 ha) = 39·2

This association lies closer along the continuum to a tropical evergreen forest than any other encountered in Karnali-Bardia. Two evergreen species which reach relatively high densities only in this association also contribute a significant amount of cover in the understory (Table 8). *Calamus tenuis*, a climbing palm, and an unidentified liana could perhaps be considered as indicators of poorly drained *Ficus-Mallotus-Eugenia* forest. Under the dense canopy and understory layer it is difficult for grasses and herbaceous plants to become established. This is clearly shown in Table 9. Visibility remains poor throughout the year largely because of the

TABLE 8

ANALYSIS OF THE UNDERSTORY IN *Ficus glomerata-Mallotus phillippinensis-Eugenia jambolana* FOREST

Species	*% Cover*	*Frequency*	*Prominence value*
Eugenia jambolana	18·0	35	106·5
Unidentified liana	11·8	22	55·3
Murraya koenigii	7·3	24	35·8
Pogostemon plectranthoides	6·4	24	31·4
Calamus tenuis	8·1	11	26·9
Clausena sp.	4·5	11	15·0
Colebrookia oppositifolia	3·2	16	12·8
Clerodendron infortunatum	2·4	11	8·0
Mallotus phillippinensis	2·4	5	5·4
Saccharum spontaneum	1·2	5	2·7
Callicarpa macrophylla	0·8	3	1·3
Aegeratum conyzoides	0·5	3	0·9

TABLE 9

ANALYSIS OF THE LOW VEGETATION IN *Ficus glomerata-Mallotus phillippinensis-Eugenia jambolana* FOREST

Species	*% Cover*	*Frequency*	*Prominence value*
Bare ground	76·2	84	698·4
Desmostachia bipinnata	8·5	15	32·9
Eugenia jambolana	2·5	10	7·9
Cynodon dactylon	2·9	4	5·8
Unidentified fern	1·9	6	4·7
Clerodendron infortunatum	1·3	6	3·2
Unidentified composite	1·3	4	2·6
Erianthus ravennae	1·3	3	2·3
Saccharum spontaneum	1·6	2	2·3
Clausena sp.	0·7	3	1·2
Imperata cylindrica	0·7	3	1·2
Lactuca sp.	0·7	3	1·2

density of the lianas. Wherever it occurs, the thorny *Calamus tenuis* severely restricts movement through the forest.

Another situation which is common in the study area is a savannah habitat dominated by the silk cotton tree, *Bombax ceiba*. The difference between a savannah and a grassland in Karnali-Bardia is associated with the degree of human interference that has previously taken place. For this reason savannah and grassland habitats lie on a continuum which may shift back and forth quite readily over time. The understory layer in both the savannah and grassland habitats is dominated by tall coarse grasses such as *Imperata cylindrica*, *Erianthus ravennae*, and *Vetiveria zyzanoides* (Table 10). While the grassland habitat may contain only a few scattered trees over several hectares, *Bombax* savannah supports a higher density and a much greater diversity of tree species (Table 11). Seven of the taller tree species reach a height of over 25 m. *Bombax ceiba* itself is the tallest tree encountered anywhere in the reserve. Its role in the successional pattern of the savannah/grassland is most important since it is resistant to fire, heavy grazing, and flooding, three factors which

TABLE 10

ANALYSIS OF SPECIES IN THE BOMBAX SAVANNAH/GRASSLAND UNDERSTORY BY THE POINT-FRAME METHOD

Species	*% Cover*	*No. of hits*	*Frequency*	*Prominence value*
Imperata cylindrica	53·4	464	53	389·8
Erianthus ravennae	10·2	88	10	32·3
Bare ground	8·7	76	9	26·1
Vetiveria zyzanoides	5·4	47	5	12·6
Aegeratum conyzoides	5·1	44	5	11·5
Cyperus sp.	3·6	31	4	6·8
Saccharum spontaneum	3·1	27	3	5·5
Unidentified grass	2·5	22	3	4·0
Desmostachia bipinnata	2·2	19	2	3·3
Cassia tora	2·1	20	2	3·2
Cynodon dactylon	1·5	13	1	1·8
Echinochloa sp.	1·0	9	1	1·0
Pogostemon plectranthoides	0·8	7	1	0·2
Digittaria sp.	0·1	1	1	0·1
Callicarpa macrophylla	0·1	1	1	0·1

TABLE 11

TREE SPECIES ENCOUNTERED IN THE *Bombax* SAVANNAH HABITAT

Most common	*Less common*
Bombax ceiba	*Lagerstroemia parviflora*
Garuga pinnata[a]	*Mitragyna parvifolia*[a]
Adina cordifolia[a]	*Albizzia odoratissima*[a]
Randia dumetorum	*Albizzia lebbek*[a]
Dalbergia sissoo[a]	*Butea frondosa*[a]
Casearia tomentosa	*Holoptelia integrifolia*[a]
Mallotus phillippinensis	*Emblica officinalis*
Eugenia jambolana[a]	*Streblus asper*
Aegle marmelos	*Gmelina arborea*
Bauhinia racemosa	
Acacia catechu[a]	

[a] = trees over 15 m.

play a major role in shaping vegetational composition in Karnali-Bardia.

Baghora Phanta (grassland), which also occurred in the study area, was created by clearing for cultivation and settlement. In areas severely overgrazed by domestic stock, unpalatable shrubs such as *Cassia tora* and *Aegeratum conyzoides* are locally dominant. *Chrysopogon aciculatus*, a grass which causes mechanical injury to grazers along with less desirable annual grasses, may increase in cover with further deterioration of the rangeland.

Visibility in the *Bombax* savannah/grassland habitat is dependent upon the period of burning. After a major fire it becomes the most open of all the habitat types previously described. During monsoon both visibility and movement remain restricted by the tall grass understory.

In recent years research into the mechanisms of alternative photosynthetic pathways has led to the discovery that a number of plant species utilise the four carbon dicarboxilic acid cycle (Black, 1973). The family which is best represented in this group is the Gramineae (Laetsch, 1974). Since a large number of tropical grasses are C_4 photosynthesisers it is thought that this photosynthetic pathway may have evolved in response to warm growing conditions. Under higher temperatures the C_4 pathway allows for an increased photosynthetic rate and a more rapid growth rate than C_3 plants under similar environmental conditions. The majority of grass species encountered in the savannahs and grasslands of the reserve have been verified as C_4 plants. These include *Arundo donax*, *Phragmites* sp., *Panicum* spp., *Brachiaria* sp., *Digitaria* sp., *Chrysopogon* sp., *Cymbopogon* spp., *Heteropogon contortus*, *Erianthus* sp., *Imperata cylindrica*, *Saccharum spontaneum*, *Cynodon dactylon*, *Paspalum distichum*, *Pennisetum* sp., *Setaria* sp., *Coix lachryma-jobi*, *Dactyloctenium aegyptium*, *Eragrostis* spp., *Themeda triandra*, *Echinochloa colonum*, and *Sporobolus* sp. (Smith & Brown, 1973). The high productivity of some of these species common to the wetter areas of the grasslands and the floodplains was demonstrated by growth measurements recorded during the monsoon. By July several tall grasses had reached a height of 2 m. At the end of September most plants had exceeded 3 m and two species had surpassed 4 m in height.

The fifth habitat type encountered was the Ecotonal Secondary Open Mixed Hardwood forest. Marked similarities in the composition of the tree layer and the grass understory layer between the above association and the *Bombax* savannah habitat were observed. Two major differences, however, led to the decision to consider this open mixed hardwood association to be a distinct habitat type. First, the density of the tree layer is high enough to qualify this habitat as forest as opposed to the scattered distribution of trees in the *Bombax* savannah. Second, a conspicuous shrub layer dominated by *Colebrookia oppositifolia*, *Pogostemon plectranthoides*, *Clerodendron infortunatum*, and *Murraya koenigii* is present, in contrast to the predominantly grass understory found in the *Bombax* savannah. Since it was believed that the presence of such a shrub understory was an important factor affecting the habitat utilisation by ungulates, this association was described separately. Visibility in this habitat type is severely hampered by the combined effects of the tall grass and shrub vegetation. As in the previously described associations, annual fires open up the understory during the hot season. With the beginning of the pre-monsoon rains, however, visibility is again reduced by the new growth.

The final habitat type to be mentioned is the *Saccharum spontaneum-Tamarix dioica* flood plain community. A detailed analysis in this habitat type had already been carried out along the Rapti River floodplain in Chitawan National Park, Nepal, in relation to a preliminary study of the habitat utilisation of *Rhinoceros unicornis* (Dinerstein, 1975). The findings from the above study and from a survey of the riparian vegetation in Karnali-Bardia indicated that the grass *Saccharum* *spontaneum* and the shrub *Tamarix dioica* were the dominant species encountered on the flood plains. Other tall grasses such as *Erianthus ravennae*, *Arundo donax*, and *Phragmites karka*, and a number of low herbaceous plants are also present in varying densities. The low vegetation, however, often disappears with the monsoon flooding and only re-emerges after the river levels have dropped once again. The taller grasses, on the other hand, are better adapted to withstand flood conditions. During such periods movement between the flood plain islands is restricted by the fast-flowing water. With its dense tall grass and shrub layer the *Saccharum spontaneum-Tamarix dioica* flood plain is one of the least open of the habitat types described. Many of the tall grasses in this habitat begin growing almost immediately after the fires.

Modifying factors of vegetational composition and succession

Before entering upon a discussion of successional relationships it would be helpful briefly to review the abiotic and biotic factors which bear a direct influence on the course of plant succession in the Terai ecosystem. Abiotic factors include the length of the monsoon, the total amount of rainfall, seasonal flooding, and soil conditions. Biotic factors which come into play stem from the previous land-use practices in the area, namely grazing of domestic stock, burning, clearing for cultivation, selective cutting of trees, logging, lopping for fodder, and thatch grass cutting.

Although there are no similar data with which to compare the grasslands of Chitawan National Park and Kaziranga National Park in the Indian state of Assam with Karnali-Bardia, it seems likely that the differences observed in the physiognomy of the grasslands might be attributable to the length of the rainy season and the total amount of precipitation. Tall grass species such as *Erianthus ravennae*, *Saccharum* spp., *Phragmites karka*, and *Arundo donax* are more representative of the grasslands of Chitawan and Kaziranga. In drier habitats, as exemplified by Karnali-Bardia, the tall grass species cover a much smaller total area than do the relatively shorter grasses. In addition, the riverain grasslands in Chitawan remain inundated for a longer period of time after the monsoon than in Karnali-Bardia. This factor may also have an effect on species composition, favouring tussock-forming perennials, a growth form which seems to be an adaptation to such moist conditions. Puri (1960) describes three different types of grasslands which may occur in response to variations in rainfall.

While the amount of rainfall may alter species composition in more subtle ways over a long period of time, seasonal flooding can bring about dramatic changes in vegetational pattern much more rapidly. Flooding of the major rivers in Nepal during the monsoon is a phenomenon which may be increasing in severity with the loss of forest cover in the mountainous regions of the country (Eckholm, 1976; Rieger, 1976). With the heavy deposition of silt on its flood plain, the Rapti River in Chitawan has at times escaped its banks, inundating the riparian vegetation. Some of the Terai rivers, including the Babai, have altered their course significantly in the last 15 years.

After the flood waters recede the silt layer is rapidly colonised by several ecologically important species, among which is *Saccharum spontaneum*. Its ability to spread over this habitat in a very short period of time is due to (1) its habit of forming extensive root systems; (2) the fact that it flowers just at the end of the monsoon; and (3) its production of numerous light seeds which are well adapted to wind and water dispersal. Once the growth of *Saccharum spontaneum* has become thick, it acts as a receptacle for the seeds of *Erianthus ravennae* and *Tamarix dioica*. The flood plain beaches also serve as a nursery for the seeds of *Dalbergia sissoo*. Flooding itself may create savannah-like habitat through deposition of silt, erosion, waterlogging, and the actual uprooting of the vegetation in forested and semi-forested areas.

The relationship between soil types and the vegetation in the Terai closely parallels the situation in northern India, where it has been described in detail (Champion & Seth, 1968). In Karnali-Bardia, as soils become more developed and stabilised, one begins to notice an increase in the diversity of the tree layer. In general what can be classified as early and mid-successional stages in the vegetational pattern occur on alluvial sands and sandy loams. Soils with a higher clay content than those found in the study area support a continuous belt of *Shorea robusta* forest. Poorly drained soils along small streams and rivers favour the development of the *Ficus glomerata-Mallotus philippinensis-Eugenia jambolana* forest.

The effects of man's activities on the vegetation of South Asia have been felt for many centuries dating back to nearly 3000 BC (Wharton, 1968). Man has utilised fire as a tool in both maintaining and creating savannah habitat, a successional stage most favourable for the grazing of domestic stock (Talbot, 1964). Natural grasslands and savannahs occur where a regular distribution of rainfall prevails throughout the year. The climatic conditions in the subcontinent are characterised by a distinct rainy season and a prolonged dry period. Therefore a true savannah climax in this region is not possible; instead, savannah is sustained by frequent burnings and domestic grazing (Richards, 1952; Bor, 1960; Puri, 1960; Wharton, 1968). In Lamkhole Phanta, located within Karnali-Bardia, I observed that the seedlings of the tree *Terminalia tomentosa* would rapidly become established in this grassland if annual burning did not occur.

Imperata cylindrica has become an important component of the vegetation on disturbed sites throughout Southern Asia. Its role in plant succession is a significant one because it responds favourably to the effects of many of the modifying factors under discussion. Where only occasional burning occurs, some of the tall grass species such as *Erianthus ravennae*, *Saccharum spontaneum*, *Saccharum benghalense*, *Themeda* sp. thrive. Along with the additional factors of either heavy livestock grazing, more frequent fires, or both combined, *Imperata cylindrica* often emerges as the dominant competitor. The reasons for its success lie in its opportunistic reproductive strategies. During a hot burn most of the existing grass cover is reduced to ashes. *Imperata cylindrica* is the only grass species to flower to any great degree within a short time after the fires. Its seeds are well adapted for wind dispersal and rapid germination. Finally *Imperata cylindrica* spreads by a tenacious rhizome, forming dense fire-resistant tussocks that make it difficult for other species to become established. These adaptations confer upon *Imperata* a definite advantage in propagation over more valuable fodder species faced with the same environmental conditions.

Within the last decade both Lamkhole and Baghora Phantas were under cultivation by local villagers. With the cessation of cultivation it was found that *Imperata cylindrica* emerged as the early dominant on old-field sites. This same pattern has been noted in Chitawan (A. Laurie, pers. comm.). Presumably if Chisapani and Amraini (the last two remaining villages still inside the borders of Karnali-Bardia) are relocated, the same successional relationship would be observed. *Imperata cylindrica* is also the most important thatch grass in the Terai and has therefore been cut annually within Karnali-Bardia. It is only in the last year that the amounts and the areas in which thatch could be cut have been regulated.

At one time logging dramatically altered the landscape in the immediate area of the reserve. In 1921 a railroad line extending north from the Indian border was built for the purpose of timber extraction. It is reported that large areas were levelled and only a portion of the timber was actually transported before the scheme was ultimately abandoned.

All factors considered, forest clearing for human settlements, and cultivation, have had the most deleterious effects on the vegetation and on wildlife habitat in the reserve area. From Thakurdwara to Barghada, large areas that were once savannah and secondary forest, and excellent habitat for the endangered tiger (*Panthera tigris*), have been transformed into rice paddies. A forest corridor which had previously extended from the southern part of the reserve to the Indian border and offered safe passage to elephant and other animal populations has been all but severed. Such habitat destruction is rather recent in origin. Prior to 1954 the threat of malaria precluded the possibilities of large-scale agricultural development in Bardia district. Only the Tharus, an indigenous tribe of the Terai, who demonstrated a marked resistance to malaria, were able to support themselves through subsistence farming in small pockets of clearings amidst the forested areas. With the advent of malaria control in 1954, however, hill tribesmen from western Nepal left their terraced hillside farms to clear potentially arable, malaria-free flat land in Bardia district. Settlements all along the southern border of Karnali-Bardia would have continued to expand into the reserve proper if the Government of Nepal had not interceded to demarcate the reserve and protect it from further encroachment.

The human population around the perimeter of the reserve is expanding. Without any system of management, human use of the adjacent forests and range lands has escalated beyond the carrying capacity of these areas. Under the combined influences of burning, overgrazing, and the indiscriminate cutting of firewood and building timbers, old growth *Shorea robusta* forest in these unprotected tracts have been reduced to parklike conditions. Continued lopping for fodder has severely hampered the regeneration of a number of tree species. Where overgrazing has reached critical levels on communal village pasture lands, unpalatable and often thorny scrub species have become highly successful invaders. The maximum seasonal biomass of domestic ungulates (buffalo, cattle, sheep and goats) that made continuous use of the study area until 1975 was estimated at 47,605 kg/km^2 (Dinerstein, in press). Now that villagers have been prevented from using the reserve as a place to graze their livestock and from gathering the forest resources they deem necessary for survival, the additional impacts on these exterior areas will be severe. Under such pressures the Karnali-Bardia Wildlife Reserve may emerge in the years to come as an island which represents a remaining example of the vegetation and wildlife once common to the western Terai.

Successional relationships

A proposed model of plant succession in the Karnali-Bardia Wildlife Reserve based upon the previous discussion is presented in Fig. 8. As expected, the effects of the modifying factors discussed above tend to revert the successional pattern back to an earlier stage of development. With the existing climatic regime, soil conditions, and modifying factors, various associations of *Shorea robusta* forest have come to dominate most of Karnali-Bardia. About 70 % of the reserve land area is at present covered in this manner. This means that less than 30 % of the reserve vegetation is represented by flood plain, grassland, savannah, and riverine forest. These ratios have a significant influence on the overall habitat utilisation of a number of important species of ungulates and carnivores in the reserve (Dinerstein, in press). Clearly if these latter less common habitat types are more suitable to the needs of Karnali-Bardia's endangered species, their preservation is essential. By correlating habitat preference with the proposed model of forest succession, wildlife managers will hopefully gain a better understanding of what effects existing environmental conditions, past land use, and future management strategies will have on the current size and distributions of wildlife populations in Karnali-Bardia.

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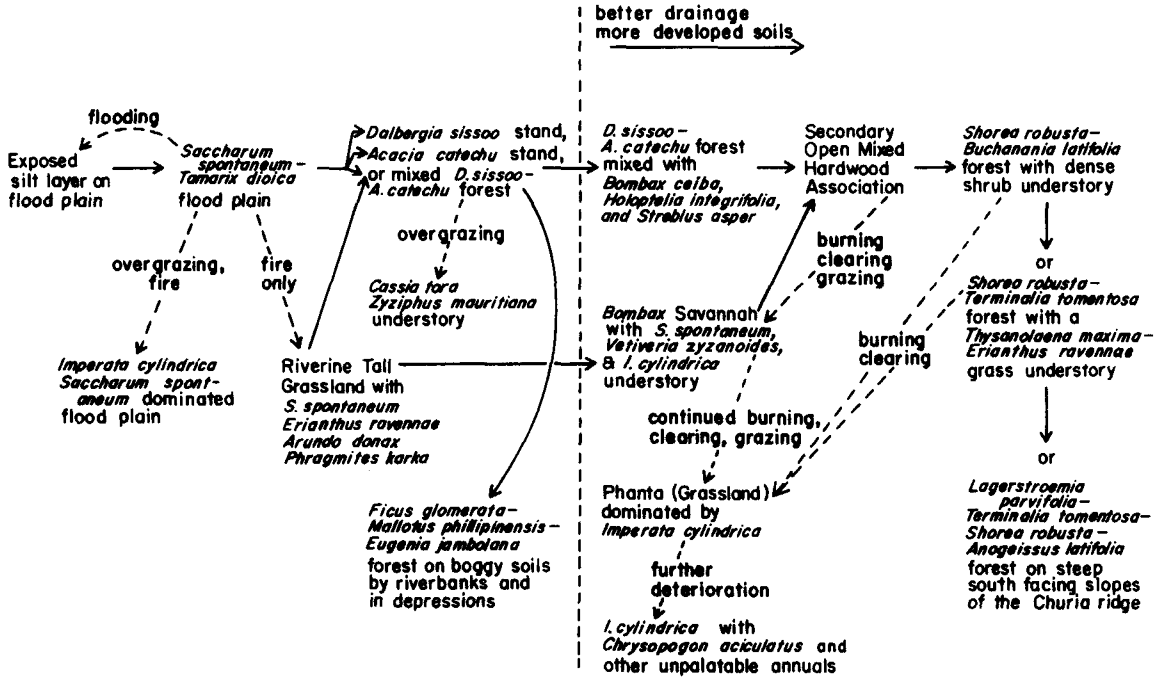

Fig. 8. Proposed pathways of successional change in the Karnali-Bardia Wildlife Reserve. The solid lines indicate the possible path of succession without biotic modifying factors being considered. Dotted lines illustrate the effects of biotic factors on plant succession. In general the direction of the dotted lines shows that biotic factors cause a shift back to earlier successional stages of development.

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