Browsing *Rhinoceros*, Stunted *Litsea*, and the Effect of a Megaherbivore on Riverine Forest Structure

by

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ABSTRACT

In Royal Chitwan National Park, Nepal, a relic population of Greater One-Horned Rhinoceros (*Rhinoceros unicornis*) browse and bend saplings of a common riverine forest tree, *Litsea monopetala* (family: Lauraceae). Results from exclosure studies reveal that repeated browsing and breaking of stems during the winter months stifle vertical growth in *Litsea*. *Litsea* foliage remains high in protein and cell solubles between Nov and Feb while the quality of other forage plants drops markedly. Cropping by *Rhinoceros* has a significant negative effect on tree height, leaf number, and angle of growth of the sapling. *Litsea* sprouts readily from stumps and browsing by *Rhinoceros* has a significant positive effect on the production of new leaves below 2 m in height. Browsed *Litsea* plants grow horizontally and vertically in response to chronic pruning. *Rhinoceros* affect sapling growth of *Dalbergia sissoo* and *Mallotus philippinensis*, two other common riparian species, in a manner similar to *Litsea*. Riparian plants avoided by *Rhinoceros* dominate the riverine forest canopy whereas stunted saplings of the most preferred species, *Litsea* and *Mallotus*, are abundant in the understorey. These data suggest that intensive browsing by giant herbivores is an important variable in determining which species and how many individuals reach the forest canopy.

Key words: Rhinoceros unicornis, Litsea monopetala, Nepal, megafauna, South Asia, ungulates, riverine forest, forest structure, herbivory

Running head: Browsing Rhinoceros and Riverine Forest Structure

Topic sentences:

1. Effects of large mammmals on vegetation structure
2. Feeding behavior of large ungulates in South Asia
3. Evolutionary role of megafauna in plant/animal interactions

INTRODUCTION

The effect of browsing by Asian megaherbivores (i.e. mammals > 300 kg) on forest structure has received little attention from ecologists, even though several species feed extensively on foliage and stems (Olivier 1978, Laurie 1978, Gyawali 1986) and distort tree growth (Mueller-Dombois 1970). The guild of giant Asian browsers includes Asiatic elephant, three species of rhinoceros, three species of wild cattle, several species of deer, and Malayan tapir. These browsers have coexisted with forest plants for millenia and chronic herbivory has probably been an important selective force in the evolutionary biology of certain plant species.

The purpose of this paper is to test the general hypothesis that large mammalian herbivores influence forest structure and canopy composition by inhibiting vertical growth of saplings which are preferred food items. Specifically, I ask if chronic browsing and bending of *Litsea monopetala* (Lauraceae) by Greater One-Horned Rhinoceros (*Rhinoceros unicornis*, hereafter referred to as rhinoceros) prevent most *Litsea* individuals from reaching the canopy. The participants in this plant/animal interaction are common members of the flora and fauna of lowland riverine forests in the Royal Chitwan National Park, Nepal (elevation 200 m). Here, I present the results of a 3 year study conducted between 1985-1988 using exclosures to protect *Litsea* saplings from rhinoceros. I also provide data on the nutritional value of *Litsea* compared to other plants eaten by rhinoceros, the amount of time spent feeding on *Litsea*, and the intensity of browsing on saplings of other common species in riverine forest. Finally, I present a forest inventory of woody stems in riverine forest to test the prediction that rhinoceros influence canopy composition by limiting vertical growth in the species upon which they most prefer to feed.

Rhinoceros/ browse plant interactions

Between 350-380 rhinoceros exist in the park (Dinerstein and Price, MS), and about 60 adults where the forest stand inventory was conducted. Between 1-6 rhinoceros/night fed on *Litsea* in the forest tract containing the exclosures.

Rhinoceros are primarily grazers (Laurie 1978, Gyawali 1986; E. Dinerstein unpubl. data) but during the winter months, they frequently browse *Litsea* and *Mallotus philippinensis* (family: Euphorbiaceae) saplings and during the hot season (March-April), heavily browse saplings of *Dalbergia sissoo* (family: Fabaceae). In certain riverine forest stands *Litsea* individuals occur in high densities and can be the most common species of sapling encountered (E. Dinerstein, pers. obs.). *Mallotus* is less common than *Litsea* but *Dalbergia* is one of the most common woody species on the flood plain islands in the Narayani River in Chitwan valley.

By the end of the winter browsing season, every *Litsea* sapling I found in the central part of Chitwan showed browse marks from rhinoceros. Adult rhinoceros weigh about 2,000 kg and many branches and saplings were bent or broken due to rhinoceros walking over saplings and bending them to the ground (E. Dinerstein, pers. obs.). Laurie (1978) observed that female rhinoceros accompanied by calves would bend large saplings positioning the most tender leaves within reach of their offspring.

Litsea is dioecious. Trees are evergreen with moderate leaf fall beginning in Nov. New leaves emerge in mid-Feb, coinciding with the period when new grass shoots emerge on the adjacent flood plain. Rhinoceros largely abandon browsing and graze heavily at this time. In response to chronic herbivory, saplings of Litsea sprout readily in Feb, issuing sprays of shoots along browsed and bent limbs and trunks and from locations where old stems have been snapped. Partially broken and bent trunks often spread horizontally in several directions.

Information on other rhino/plant interactions can be found in Dinerstein and Wemmer (in press) and Dinerstein (in press) and on the large herbivore fauna in Dinerstein (1987), Seidensticker (1976) Mishra (1982), and Laurie (1978).

METHODS

Ingestion of Litsea by rhinoceros during the year

I estimated the relative importance of Litsea in rhinoceros diets by observing the feeding behavior of radio-collared animals over 49 24 periods sampled in every month of the year. Together with the field staff of SI/NTEP, we recorded the activities of each focal animal at 5 min intervals. The total number of 5 min observations during which rhinoceros fed on Litsea was divided by the total number of 5 min intervals noted as feeding observations. During the main Litsea browsing season itself, 6 and 8 activity watches were conducted for males and for females, respectively. Data were analyzed separately. Home ranges of most of the rhinoceros chosen for these studies included the area where I set up rhinoceros exclosures and where fecal analysis of rhino diets was conducted (Gyawali 1986). For fecal analysis, fresh dung samples from 20 latrines were collected monthly from the study area. Fecal material was washed to obtain plant cuticles, and mounted on slides (5 slides/monthly sample) (Gyawali 1986), and analyzed along transects using the line-intercept method (Seber and Pemberton (1979).

<u>Nutritional value of Litsea vs. other forages</u>

Mimicking the manner in which rhinoceros browse <u>Litsea</u>, I harvested a number of random rhinoceros bites from <u>Litsea</u> saplings each month. At least 25 other plants and plant parts sought out by rhinoceros, occasionally eaten, and avoided by rhinoceros each month were also included in the nutritional analysis of rhinoceros forages. Two distinct samples were collected for each plant or plant part analyzed and data presented are the mean values. Samples were dried at 60° C. for 48 hr and ground in a Wiley Mill to pass through a 1 mm mesh screen. Samples were stored in labelled Whirl-Pak bags and shipped to the the Wildlife Habitat Lab at Washington State University. Fiber analysis was conducted according to Goering and Van Soest (1970) and Mould and Robbins (1981). Crude protein analysis (Kjeldahl N x 6.25) was conducted according to AOAC (1965).

<u>Selective inhibition of Litsea by rhinoceros</u>

To test the hypothesis that rhinoceros inhibit <u>Litsea</u> saplings from reaching the canopy, I located 12 10 x 10 m plots in a riverine forest where <u>Litsea</u> occurs in high densities. I randomly assigned six plots to be open to foraging rhinoceros and six plots to be protected from rhinoceros. These plots were erected and all initial measurements made in October of 1985. At least 25 Litsea saplings were marked within each plot. Prior to erecting a wooden-fence around the six protected plots, a student t-test on one variable, sapling height, and a Mann-Whitney U_c test on angle of growth (proportion of stems growing upright/plot) revealed no significant difference between plots assigned as protected and unprotected. At the end of three browsing seasons, I tested for differences between mean sapling height and angle of growth for marked saplings in unprotected and protected plots. For the angle of growth data I used an arc-sine transformation to test for differences between proportions of straight stems in protected and unprotected plots.

Density of the browse volume

To quantify defoliation of Litsea by rhinoceros, I counted the number of leaves on 10 saplings per plot on four unprotected plots and four protected plots prior to and after the browse season. I used the arc sine transformation on raw data to test for differences between the proportion of leaves removed by browsing rhinoceros versus natural leaf fall. To test the hypothesis that rhinoceros browsing alters the amount of leaf tissue available below 2 m (where leaves are readily accessible), I counted the number of branches supporting at least 10 entire leaves < 2 m above the ground. I randomly selected 10 saplings/plot for this comparison. Like in other members of the Lauraceae, the foliage of Litsea is clustered at the tips of the branches.

For all of the above variables measured, I calculated mean values from marked saplings in each of the six protected and the six unprotected plots. I then conducted non-parametric tests using the mean values.

Suppression of vertical growth among riverine forest plants

To test the prediction that browse preference by rhinoceros influences the probability that saplings of a given species will reach the canopy, I surveyed 10 0.5 ha plots located in five patches of riverine forest. All woody stems encountered were classified as either eaten or not eaten by rhinoceros and whether or not they were small enough to be bent over and browsed by rhinoceros (accessible understory) or not (inaccesible overstory). Along flood plains where Dalbergia was common, I walked transects and merely recorded the percentage of stems which had been bent and browsed by rhinoceros.

RESULTS

Consumption of Litsea by rhinoceros

Fecal analysis of diets from a rhinoceros population in Chitwan revealed that Litsea was a primary food source in September and from November through February and eaten in trace amounts the remainder of the year (Table 1). Twenty-four hour activity watches during the winter browsing period showed no significant difference between adult males and females in consumption of Litsea (N= 6,8 Mann-Whitney U (MWU)=37; p>0.10). Pooled data from 14 watches revealed that feeding time on Litsea averaged 10.0% of all recorded feeding observations (sd = 12.33, range = 0.0 - 42.6%) over 24 hr.

Nutritional value of Litsea vs. other forages

A rhinoceros "mouthful" of Litsea was relatively high in %

crude protein (N x 6.25) averaging 17.4% dry wt over the year (Table 1). Among common rhinoceros forage plants, only the leaves of two trees, *Mallotus philippinensis* and *Dalbergia sissoo*, and the shrub *Callicarpa macrophylla*, ranked higher (E. Dinerstein, unpubl. data). The cell soluble fraction of *Litsea*, (i.e. the easily digestible materials minus the cellulose, hemicellulose, lignin, and silica) was also higher than in regrowth and mature leaves of the grass, *Saccharum spontaneum*, the food source most commonly found in rhinoceros diets during the winter (Table 1). Percent water content of new *Litsea* leaves averaged 74% (sd = 2.2%, N = 4) and 59% for mature leaves (sd = 1.1% N = 4).

Inhibition of vertical growth of *Litsea* by rhinoceros

Exclosure studies revealed that browsing and trampling by rhinoceros had a significant negative impact on sapling height (MWU=36 N= 6,6 $p<0.005$). Whereas the results presented here are from measurements made after three browsing seasons, it should be noted that differences in sapling height were significant after protection during one browsing season. The grand mean for sapling height for all protected plots was 4.9 m; 31 protected saplings were between 6-7 m tall, 11 saplings between 7-8 m, and 4 saplings exceeded 8 m in height. In contrast, the grand mean for unprotected saplings was 2.7 m. In protected plots nearly all saplings that were bent or prostrate at the start of the experiment were vertical or near vertical after two growing seasons. Marked stems of protected saplings grew significantly more straight (MWU=36 N= 6,6 $p<0.005$). I found no significant difference in the number of dead marked saplings between protected and unprotected plots (MWU=25 N=6,6 $p>0.20$).

Density of the browse volume

Protected saplings lost only about 35% of their leaves due to natural leaf abscission during the winter months. In contrast, unprotected plants lost a mean of 76% of their leaves to browsing rhinoceros, a significant portion of the foliage (MWU=16 N=4,4 $p<0.05$). This grand mean value also incorporated leaves that may have fallen off the tree when rhinoceros trampled it. In some unprotected plots, saplings were completely defoliated.

Browsing and trampling had a significant positive effect on the production of new leaves and stems below 2 m. Saplings chewed and pruned by rhinoceros produced significantly more leafy shoots below this level than did unbrowsed saplings (MWU= 36 N=6,6 $p<0.005$). Most of the new growth on protected saplings was distributed at the upper edge of the crown.

Browsing and woody stem height survey in riverine forests

Six species of trees were common in riverine forest along Chitwan's Rapti River (Table 2). Woody stems that as saplings were avoided by rhinoceros, dominated the canopy and subcanopy whereas the most heavily browsed species, Litsea and Mallotus, ranked last and next-to-last, respectively. In the accessible understory, i.e. those woody stems still vulnerable to bending and trampling by rhinoceros, the number of the two most preferred stems (Litsea and Mallotus) nearly equalled the total number of stems from species not browsed by rhinoceros. Differences in the ratio of browsed to unbrowsed stems in the two "strata" were highly significant (χ^2=916.9 df= 1 $p< 0.001$).

In areas where *Dalbergia* saplings are abundant, rhinoceros also stifled vertical growth of this species. On a small island in the Narayani River adjacent to an area supporting at least 32 rhinoceros, I observed that 100% (N= 150 saplings) of all young *Dalbergia* were bent prostrate and defoliated. Likewise, along a 1 km transect through a grassland in eastern Chitwan supporting about 10 adult rhinoceros, I observed that 95% (N=103) of all saplings had been heavily browsed and bent.

DISCUSSION

Rhinoceros preference for *Litsea*

Rhinoceros seek out *Litsea* saplings during the winter and by Feb nearly all plants show signs of browsing. Thus, calculating a preference index for *Litsea* is unnecessary. Nonetheless, rhinoceros reduce intake of *Litsea* by mid-Feb even though foliage continues to remain high in crude protein and cell solubles. I attribute the change in diet selection to forage availability and foraging efficiency. By mid-Feb or March, the dense new shoots of the flood plain grass, *Saccharum spontaneum*, are easily harvested by rhinoceros whereas many reachable *Litsea* saplings have been stripped of leaves. For a bulk feeder with a high forage intake, time constraints may prohibit feeding on more than a few mouthfuls of the more nutritious but scattered *Litsea* foliage in favor of the lower quality but more abundant grasses. Circumstantial evidence in support of this supposition is that six captive calves less than one yr old all preferred equal-sized bundles of newly flushed *Litsea* leaves over *Saccharum spontaneum* and other common grasses during the period when free-ranging rhinoceros are grazing heavily but when *Litsea* saplings are still recovering from heavy browse damage (E. Dinerstein pers. obs.).

The impact of rhinoceros on riverine forest structure

Chronic herbivory by animals affects tree architecture (Whitham and Mopper 1985, Mueller-Dombois 1971) and vegetation structure (Owen-Smith 1987; Janzen 1986). Exclosure studies in Chitwan clearly demonstrate that rhinoceros stifle vertical growth of Litsea. Browsed plants also differed from unbrowsed plants in shape: protected Litsea saplings grew straight and unprotected Litsea saplings exhibited characteristic stunted crowns.

Data from this study show that the impact of rhinoceros on riverine forest trees is not limited to Litsea as two common species, Dalbergia sissoo and Mallotus philippinensis, are heavily browsed and trampled. During March and April, the young leaves of Dalbergia, which are higher in crude protein (33% dry weight) than any plant in Chitwan, are often defoliated by rhinoceros. Laurie (1978) also noted intense pruning of Dalbergia saplings by rhinoceros. The biological significance of these interactions can also be studied by reintroducing rhinoceros to habitats where they once occurred and to look for changes in growth forms of preferred browse species such as the three species mentioned above. During 1986, SI/NTEP, in association with the His Majesty's Government of Nepal, relocated 12 rhinoceros to the Royal Bardia Reserve in western Nepal, an area where rhinoceros have been absent for a minimum of two centuries (Mishra and Dinerstein 1987). In Bardia, Litsea is an uncommon tree, but Dalbergia is the most common tree on the flood plain and _Mallotus_ is the most common tree species in riverine forest (Dinerstein 1979, 1987). I predict that with the reintroduction of rhinoceros, vertical growth of flood plain forests dominated by _Dalbergia_ and saplings of _Litsea_ and _Mallotus_ will be stifled in a manner similar to that observed in Chitwan.

Despite heavy browsing and trampling by rhinoceros, some _Litsea_ saplings do reach the forest canopy. Nevertheless, all of the adults encountered in the forest survey had crooked boles, a result of previous browsing. Rhinoceros walk over and ride to the ground _Litsea_ stems less than 15 cm dbh. I suggest that the manner that browsed and trampled saplings eventually escape rhinoceros is to develop a thick trunk that exceeds 15 cm at a height of 2 m and to send out a spray of branches from broken trunks. If new stems emanate from a number of directions, they will shield at least one interior stem from rhinoceros. Protected _Litsea_ stems grow quickly and within three years grow thick and tall enough to escape browsers. I speculate that intensive cropping by large mammals on plants like _Litsea_ may have contributed to the loss of apical dominance in favor of stump sprouting. By coppicing from many locations, at least one interior stem may have a chance for sufficient vertical growth and avoid being eaten by a megaherbivore.

A walk through a riverine forest at the end of Feb in Chitwan quickly reveals the impact of browsing rhinoceros. In patches where _Litsea_ and _Mallotus_ are common, the first stratum is dominated by stunted saplings. A large vertical gap is visible in the mid-canopy, a space which in the absence of rhinoceros would be occupied by saplings of these two tree species. The intensity of the bending and browsing seems more characteristic of the impact of an herbivore population at an outbreak stage. However, the rhinoceros population in Chitwan, decimated by poaching, began increasing again only in the late 1960's and is still below carrying capacity (E. Dinerstein, unpubl. data). Even at reduced population levels, the interactions described here between rhinoceros and woody plants clearly suggest the evolutionary legacy of large mammals in shaping forest structure.

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Table 1. Use of Litsea by rhinoceros, percent crude protein and cell soluble fractions (dry weight) of Litsea (Limo) compared to Mallotus philippinensis (Maph), Dalbergia sissoo (Dasi), and Saccharum spontaneum (Sasp)

	Litsea as % of monthly diet*	% crude protein						% cell soluble fraction***				
		Limo	Maph	Dasi	Sasp regrowth** or new shoots	Sasp stem	Sasp mature leaves	Limo	Maph	Dasi	Sasp regrowth** or new shoots	Sasp mature leaves
Jan	12.2	17.2	17.9		10.1	1.1	6.1	43	50		23	25
Feb	9.7	16.6	13.3	33.5	6.6	3.5	3.1	47	49	74	22	19
Mar	1.1	21.9	13.2	28.5	12.8	1.6	5.0	37	56	60	29	26
April	0.0	19.3	14.7		11.4	nd	nd	39	49		22	na
May	0.2	15.6	14.1		nd	nd	8.4	39	49		nd	20
June	0.2	17.9	13.7		nd	nd	7.1	41	53		nd	23
July	0.0	18.0	13.4		12.1	nd	10.0	39	44		26	25
Aug	2.3	19.5	15.4		9.5	2.6	8.5	36	42		23	23
Sep	5.5	18.7	14.6		12.8	2.2	7.7	38	46		18	19
Oct	1.3	nd	15.4		12.2	2.2	6.8	nd	45		17	17
Nov	6.1	15.2	14.1		11.5	1.3	5.0	38	43		18	18
Dec	3.8	17.1	14.3		9.7	0.9	7.3	36	43		22	24

* as determined by fecal analysis (Gyawali 1986)

** regrowth referring to new Sasp leaves emerging from stems cut for domesticated elephant fodder

*** = 100% - % remaining after conducting neutral detergent fiber wash

nd = no data: plant part either not sampled or not common due to burning

Table 2. Results of a forest survey in 2.5 ha of riverine forest. Tree species with fewer than 4 stems encountered not included (N=5). Species browsed and bent by rhinoceros are designated with an asterisk.

Species:	Inaccesible Overstory	Accessible Understory
Litsea monopetala*	30	544
Mallotus philippinensis*	40	67
Trewia nudiflora	451	103
Ehretia acuminata	202	496
Bombax ceiba	52	2
Premna obtusifolia	76	10