

FRUITS *RHINOCEROS* EAT: DISPERSAL OF *TREWIA NUDIFLORA* (EUPHORBIACEAE) IN LOWLAND NEPAL¹

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Abstract. To document the dispersal of the fruits of the tropical tree *Trewia nudiflora* by a large herbivore, we examined several aspects of the *Trewia nudiflora*–*Rhinoceros unicornis* interaction. The fruits of *Trewia nudiflora* (Linn.) (Euphorbiaceae), a common riverine forest tree of southern Nepal, are large, hard, and dull-colored upon ripening. Although unattractive to arboreal and volant frugivores (monkeys, bats, and birds), *Trewia* fruits are eaten by greater one-horned Asian rhinoceros (*Rhinoceros unicornis*). During the rainy season (June–October), *Trewia* fruits become an important food source for rhinoceros.

Trewia seeds remained from 3 to 7 d inside the gut of captive rhinoceros, but gut treatment itself had no significant effect on germination success. Manuring of seeds in dung significantly increased seedling growth.

Trewia is shade-intolerant; despite abundant fruit fall and reasonable seed germination, seedling recruitment was poor under the forest canopy. Uningested fruits often remained hard throughout the monsoon, preventing seeds from germinating. Seeds defecated into grassland latrines created by rhinoceros developed into robust seedlings, whereas seedlings on forest latrines generally died soon after germination or after the monsoon.

Heavy seed loads in dung, low germination from uningested fruits, and rapid growth of *Trewia* seedlings on grassland latrines demonstrate the role of rhinoceros in dispersal and recruitment of woody species in riverine grasslands and the significance of megafaunal dispersal.

Key words: flood plain; frugivory; India; megafauna; Nepal; *Rhinoceros unicornis*; seed dispersal; South Asia; *Trewia nudiflora*; ungulates.

INTRODUCTION

Janzen and Martin (1982) proposed that the extinct Neotropical megafauna once played a major role in the dispersal of the woody flora. Furthermore, they argued that long coexistence between Neotropical plants and large frugivores molded the evolution of fruit and seed traits of some plants for consumption and dispersal by large mammals. Because the demise of the gomphotheres, horses, proboscideans, ground sloths, and other large ungulates in the western hemisphere prohibits a direct test of hypotheses related to seed dispersal, Janzen (1981a, b, 1982a) employed domestic horses and cattle as surrogate Pleistocene frugivores. Experiments with these animals and observations with a captive, native megafauna suggest the evolutionary importance of large frugivores in the demography and microdistribution of Neotropical plants (Janzen 1981c, 1982b). This interpretation has been challenged (Howe 1985). In contrast, data on frugivory and seed dispersal by

native, large mammals in Africa and Asia, essential to evaluate the significance of megafaunal dispersal, are mostly lacking (E. Dinerstein, *in press*).

The purpose of this paper is to document the dissemination of *Trewia nudiflora* (Euphorbiaceae) by an extant large herbivore, the greater one-horned Asian rhinoceros (*Rhinoceros unicornis* Linn., referred to as rhinoceros) in Royal Chitwan National Park, Nepal. *Rhinoceros* is one of the most ancient of extant species of large mammals, with fossil records of closely related species dating back to the upper Pliocene. Rhinoceros are highly endangered. Populations of > 50 individuals occur in only two South Asian reserves: Chitwan Park in Nepal (380–400 rhinoceros; E. Dinerstein, *personal observation*) and Kaziranga National Park in Assam, India (1500 animals; E. B. Martin, *personal communication*).

Rhinoceros and *Trewia* occur in high densities along the flood plains of Chitwan. During the monsoon (June–October) *Trewia* ripens fruit in abundance in Chitwan's riverine forests. Ripe fruits on the tree are ignored by bats, birds, and monkeys but are devoured by rhinoc-

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TABLE 1. Characteristics of *Trewia nudiflora* fruits.

	Mean	SD	N
Wet mass (g)	26.0	4.6	75
Diameter (mm)	37.8	9.3	75
No. of seeds/fruit	3.2	0.9	75
Mass of seeds (g)	0.4	0.1	20
Seed diameter (mm)	7.8	0.7	14
Water content of pulp (%)	83.8	0.5	8
Pulp/seed ratio (wet mass)	8.4	1.4	8

eros, and to a lesser extent are eaten by deer and domestic cattle when fruit falls to the ground. The frequent occurrence of luxuriant mats of *Trewia* seedlings on rhinoceros latrines in grasslands led to our working hypothesis that rhinoceros were the major dispersal agents of *Trewia* in Chitwan and an important vector for the establishment of this species on the flood plain.

In this paper we describe various aspects of the rhinoceros-*Trewia* interaction. Specifically, we consider gut passage rates of *Trewia* seeds through rhinoceros, seed survival through the gut, ingestion rates, effects of seed swallowing and manuring on seedling vigor, rhinoceros-generated seed shadows, the fate of uningested seeds and fruits, and the factors controlling establishment of *Trewia* on rhinoceros latrines on the flood plain. We also examine the distribution of *Trewia* in the absence of rhinoceros and in areas where domestic livestock occur.

THE NATURAL HISTORY OF *TREWIA* FRUITS

Large fruit size (Table 1) and a hard endocarp (about the texture of a green potato in ripe fruits) distinguish *Trewia* from nearly all other fleshy fruits available in Chitwan (E. Dinerstein, *personal observation*). Ripe fruits are yellowish-green to brown and extremely bitter to our taste. The force required to crush *Trewia* seeds (143 N) is not great, but the hard endocarp of the entire fruit resists cracking. On a hard surface the force exerted by gravity on a 77.0-kg human (755 N) could not split open fruits, but many fruits are split when stepped on by elephant and rhinoceros.

Trewia is the most common tree in riverine forest, accounting for 48.5% of all stems >3 cm diameter at breast height (dbh) on a 1-ha plot (65 stems/ha). *Trewia* is dioecious; a random 1-ha sample in riverine forest yielded 118 females, 96 males, and 88 trees 4–10 cm dbh that did not flower during the census and could not be sexed. Diameter at breast height of reproductive females ranged from 6.0–57.2 cm $\bar{X} \pm SD = 24.5 \pm 11.3$ cm) and from 4.0–65.2 cm in males (21.2 ± 10.6 cm). Average fruit crop size was 70.2 fruits per tree ($N = 50$, range = 2–1615 fruits). Fruits begin to ripen during the early monsoon (June) and peak availability occurs in the mid-late monsoon (July–August) (Fig. 1). Ripe fruits undergo a slight color change and fall to the ground. By late August, the high density of *Trewia*

trees ensures that fruit carpets the forest floor in the study area.

METHODS

Ingestion of Trewia by wild rhinoceros

We measured daily consumption of *Trewia* by observation of radio-collared rhinoceros during 24-h activity watches. This and all other activities and experiments were conducted between 1984 and 1986. When possible we counted the number of fruits ingested during 5-min intervals by approaching on elephant back to habituated rhinoceros and observing feeding through binoculars. When intake could not be determined accurately, we simply recorded feeding on *Trewia* and expressed it as a frequency of feeding observations in a 24-h period.

An index of monthly consumption was estimated by randomly selecting 20 1-kg dung samples each month from grassland and forest latrines and counting the number of intact and cracked seeds present in the dung.

Seed passage experiments with a captive rhinoceros

Fruits fed to the captive rhinoceros were collected in the morning in Chitwan and transported to the Kathmandu zoo the same day or the following day. Because rhinoceros regularly eat fallen fruit at least several weeks old, we assume the 1-d delay in feeding had no effect on the experiment. In the first feeding trial the rhinoceros ingested 114 fruits during a 10-min interval; in the second trial we fed it 300 fruits, which were ingested within 54 min.

After the fruits were ingested, we collected the dung excreted in each bout and deposited dung in numbered, plastic bags, recording the date and time of defecation of each sample. We searched for and removed *Trewia* seeds the same day the dung was excreted. The black, shiny *Trewia* seeds stood out against the bright green excreta, and we felt we missed few intact seeds passed by the rhinoceros. We also recorded mass of feces and

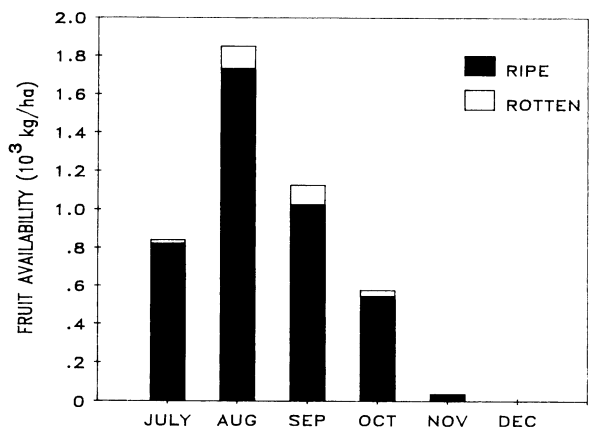


FIG. 1. Biomass of ripe and rotten *Trewia* fruits on the forest floor.

number of intact and broken seeds passed in the dung. Fecal material was searched until we had examined at least 3 d worth of dung subsequent to the first bout that yielded one intact seed.

Germination and growth experiments

To distinguish the effects of gut treatment from the effect of manuring on germination rate and seedling growth, we randomly assigned defecated and uningested seeds to be planted in dung and in seed-free soil. The experiment, a 2×2 factorial design, was conducted during the peak *Trewia* fruiting period in an open area. Randomly located replicates were housed in 0.50-m² screened boxes protected from insect seed predators by frequent application of an effective chemical insecticide (Finit). Intact seeds randomly selected from rhinoceros latrines and from entire, ripe fruits were exposed to four treatments: 60 seeds defecated by rhinoceros and planted in 20 kg of dung; 60 seeds defecated by rhinoceros and planted in forest topsoil; 60 uningested seeds planted in dung; and 60 uningested seeds sown in forest topsoil. Each treatment was replicated three times.

The number of seeds germinated (i.e., cotyledon emerging from the seed coat) was noted daily. At the end of the growing season, 51 d later, we carefully removed seedlings. Wet mass of leaves, stems, and roots were recorded for each seedling. Plant parts were dried at 70°C for 48 h to obtain dry mass.

Seed shadows and defecation

We determined daily movements and defecation patterns of rhinoceros by following radio-collared animals during 24-h periods. Hourly locations and defecation sites were marked on acetate overlaying aerial photos of the study area. After each defecation, the feces were placed in a plastic bag and weighed using a 10-kg Pesola spring scale.

Fruit rot and the fate of uningested fruits

We estimated monthly availability of ripe and rotting fruits by counting all fruit on 10 100-m² forest plots and weighing ripe and rotten fruit separately.

Trewia seeds may emerge from the hard endocarp via ingestion or by being crushed when rhinoceros or elephant step on them. To determine the effects of fruit crushing by large mammals on seed germination, we observed the extent to which fruits were crushed by rhinoceros and elephant, and simulated the effect. We randomly placed 20 0.5-m² screened-in enclosures, 10 in the forest and 10 in short grassland. Using a randomized block design, we assigned 100 crushed fruits to one side of the divided box and 100 entire fruits to the other side. We recorded the number of seeds that germinated from each side of each replicate on a weekly basis and recorded seedling height after 51 d.

*Latrine florae and recruitment of *Trewia* on natural latrines*

We measured plant cover at 37 grassland latrines using the line intercept method (Canfield 1941). A total of 306 m was sampled along intercepts. Sampling was stratified vertically to distinguish between seedling cover, sapling and shrub cover, and tree cover. We restricted sampling to only actively used latrines >1 m in diameter. Most latrines measured were elliptical in shape and averaged 7 m along the longest axis. Sampling was conducted on 28 August, when annual growth was nearing its peak. To evaluate recruitment on grassland and riverine forest latrines we measured seedling number and height on randomly located, 1-m² plots on 30 grassland and 30 forest latrines.

*Recruitment of *Trewia* on experimental latrines*

To evaluate light limitation as a mortality factor for *Trewia* seedlings, we created experimental latrines: 10 replicates in short and intermediate grasslands and 10 under the riverine forest canopy. We added 20 kg of fresh dung monthly to each experimental latrine after deposition of an initial base of 180 kg. These amounts seemed appropriate based on our observations of deposition patterns and size of natural latrines, although later observations indicated that our estimates were conservative. Open-mesh fencing around experimental latrines excluded intermediate-sized and the large herbivores and protected seedlings from fire. We recorded seedling number and height for all seedlings in randomly located 4-m² plots on paired forest and grassland latrines at the end of two growing seasons.

To determine effects of sun vs. shade on seedling growth, we germinated 50 seedlings each in 20 "sun" latrines (equal to two defecations) randomly located in various grassland types and 14 "shade" latrines randomly located under the canopy of riverine forest. In each latrine, 100 seeds were planted in dung; when seedlings had produced three leaves, we weeded plots to 50 individuals or a density of ≈ 1 seedling/100 cm². We recorded mortality twice weekly until the end of the growing season (mid-November), when we measured height of surviving seedlings.

Recruitment under the canopy

Trewia-dominated riverine forest often occurs in distinct patches. We randomly located 20 25×15 m plots among three of these patches and recorded dbh of all trees, saplings, and woody climbers >3 cm in diameter. We also tallied the diameters of all *Trewia* saplings >2 m and the heights of all seedlings within the plots, classifying seedlings as 1, 2, or 3 yr old.

RESULTS

*Consumption of *Trewia* by wild rhinoceros*

Twenty-four-hour activity watches ($N = 26$) revealed that daily consumption of *Trewia* peaked in the mid-

morning just after rhinoceros emerged from a 2–3 h wallowing period. Fruit intake was high beneath trees bordering on forest wallows. The total number of fruits ingested during 5-min sampling periods was accurately determined for five 5-min periods; intake average (\pm SD) was 17.6 ± 3.58 fruits per period (range = 14–23). On eight 24-h watches conducted in riverine forests and grasslands during the monsoon, ingestion of *Trewia* accounted for $12.4 \pm 6.3\%$ of all feeding observations (range = 7–27%). Assuming that 17.6 fruits per 5-min period was representative of the rate of fruit intake, individual rhinoceros ingested ≈ 197 fruits (or wet mass of 5.1 kg) per 24 h during the peak fruiting period.

The mean number of *Trewia* seeds per kilogram of dung collected monthly from 20 randomly sampled latrines provided an index of *Trewia* consumption over the fruiting season. The mean number of intact seeds per kilogram of dung increased in July and August, peaked in September, and declined thereafter (Fig. 2).

Gut passage and seed survival

In the first feeding trial, 114 fruits were ingested in 10 min. The first seeds emerged in the dung 46 h after ingestion, peak passage occurred 64–88 h, and the last intact seeds were passed 172 h (7 d and 4 h) after ingestion. Three hundred fruits were ingested in 51 min during the second trial (Fig. 3). Seed passage rates for the two feeding experiments were significantly different (Kolmogorov-Smirnov two-sample test, $P < .05$).

By multiplying the mean number of seeds per fruit (3.2) by the number of fruits fed to the rhinoceros, we estimated that ≈ 365 seeds were ingested in the first trial and ≈ 960 seeds in the second. Assuming that all intact seeds passed were discovered, seed mortality was 26.7 and 47.7%, respectively, for the first and second trials. Seed coat fragments also appeared in the dung.

Effect of gut passage and manuring on germination and seedling growth

Gut treatment, manuring of seeds in dung, and the interaction of the two factors did not have a significant effect on germination of *Trewia* seeds (Kruskal-Wallis two-way ANOVA, $N = 3$, $P > .05$). We included gut passage as a treatment effect along with manuring of seeds because it seemed plausible that if ingestion hastened germination, young plants grown from passed, intact seeds would have a headstart on uningested seeds. Manuring of seeds in dung had a significant positive effect on aboveground dry mass (Kruskal-Wallis ANOVA, $N = 3$, $H = 8.308$, $P < .005$) and on dry leaf mass ($H = 8.308$, $P < .005$), but not on dry root mass ($H = 1.442$, $P > .10$). Taproots from seedlings grown in dung were significantly shorter than those from seedlings germinated in soil ($H = 8.308$, $P < .005$). Root tissues for seedlings grown in dung remained concentrated in the dung layer, whereas plants grown in soil sent down longer taproots. Gut treatment had no effect

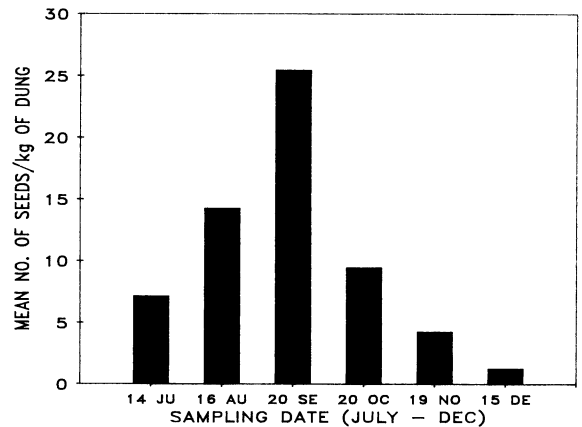


Fig. 2. Mean number of intact *Trewia* seeds per kilogram of rhinoceros dung by month.

on aboveground dry mass of seedlings, dry leaf mass, taproot length, and dry root mass. No significant interaction effects on plant growth were observed between gut treatment and manuring of seeds.

Fruit rot and fate of seeds from uningested fruits

Entire fruits placed in the sun rotted in significantly greater numbers than the same number of fruits placed on the forest floor (Mann-Whitney U test, $N = 10$, $U = 80$, $P < .05$). Removing seeds from the hard endocarp by simulating crushing by pachyderms had a significant positive effect on germination number (non-parametric [NPAR] randomized block ANOVA, $N = 10$, $P < .05$; Zar 1984:228) and seedling height (NPAR randomized block ANOVA, $N = 10$, $P < .01$). Placement of the fruits in the sun also had significant positive effects on germination (NPAR randomized block ANOVA, $N = 10$, $P < .001$) and seedling height (NPAR randomized block ANOVA, $N = 10$, $P < .001$). Only two seedlings survived after 76 d from a potential total of 3200 seeds used in the experiment in the replicates placed in the forest shade. These seedlings were both < 16 cm in height and possessed only three small leaves; rarely did marked seedlings of such low stature survive until the following monsoon, and only 1 of the 26 seedlings from the crushed fruits exceeded 16 cm. Observations on mortality of *Trewia* seedlings revealed that seedlings under 16 cm, which usually consist of a small stem, the two cotyledonous leaves, and a small third leaf, rarely survived the cool season and dry season following the monsoon (E. Dinerstein, *personal observation*).

Effect of deposition site on seedling growth and mortality

Seedlings on natural grassland latrines were far more abundant and grew more vigorously than seedlings on forest latrines (Mann-Whitney U tests with normal approximation: $N = 30$, $Z = 5.582$, $P < .05$; and $N =$

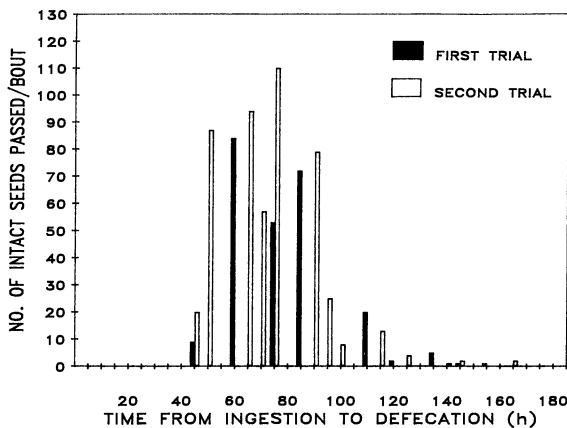


FIG. 3. Transit times for *Trewia* seeds passed by a captive rhinoceros during two different feeding trials.

30, $Z = 3.877$, $P < .05$, respectively). A combined total of only 54 seedlings was found on 30 forest latrines at the end of the growing season, whereas 529 survived on the 30 grassland latrines. Of the 54 seedlings on the forest latrines, only 11 had exceeded the cotyledonous leaf stage as opposed to 227 for the grassland latrine plants.

On 2-mo-old experimental latrines, a significantly greater number of seedlings survived the monsoon until the end of the growing season on sun rather than shade plots, where most of the seedlings died within 4 wk after emergence (Mann-Whitney U test, $N = 20, 14$, $U = 239.5$, $P < .001$). Seedlings grown in sun were also significantly larger than those grown in shade ($N = 20, 14$, $U = 280$, $P < .001$). Of the 600 seedlings planted in the forest plots, only 3 (12.5%) of the 24 seedlings that survived exceeded 16 cm, whereas 498 (85.4%) of the 1000 seedlings planted in grasslands exceeded 16 cm.

Similarly, seedlings on 2-yr-old experimental grassland latrines occurred in higher numbers (Mann-Whitney U test: $N = 10$, $U = 100$, $P < .001$) and grew significantly taller ($N = 10$, $U = 90$, $P = .002$) than on forest latrines. Most striking is that 19% of the seedlings ($N = 1037$) that survived on grassland latrines exceeded 50 cm, and 3% exceeded 2 m in height.

Rhinoceros defecation rates, dung mass, and seed deposition

The 5-yr-old captive rhinoceros that was used in the feeding experiments defecated 2–3 times/24 h (mean

TABLE 2. Age and height of *Trewia nudiflora* seedlings at the end of the growing season under the riverine forest canopy. Area sampled = 0.75 ha.

Seedling age/ht	No.	Density (no./ha)
First year < 16.0 cm tall	429	572.0
First year > 16.0 cm tall	126	168.0
Second year	68	90.7
Third year	2	2.7

= 14.7 kg/bout). Mean (\pm SD) dung mass per bout in wild rhinoceros during fruit fall in *Trewia* was 11.1 ± 6.7 kg, range = 3.7–24.3 kg, $N = 9$. Thirty percent of all observed defecations occurred in grasslands, and 56% occurred in riverine forest during the *Trewia* fruiting season ($N = 23$ defecations observed during 24-h watches).

Presence of *Trewia* vs. other plant species on grassland latrines

Although four grasses were frequently encountered at latrine sites, the plants that contributed most to percent cover were the annual legume *Cassia tora* (Leguminaceae) (32.4%), an abundant weed in overgrazed pastures and scrub outside the park, and *Trewia* (seedlings, 24.1%; saplings and trees, 11.8%). On latrines > 3 km from croplands, *Cassia* and other annuals were rare to absent, and *Trewia* seedlings dominated. Overall, we encountered 38 species, including 4 trees, 5 grasses, 16 shrubs, 6 herbaceous plants, and 7 herbaceous climbers.

Recruitment of *Trewia* under the canopy

Recruitment of *Trewia* seedlings under the canopy was remarkably low (Table 2). The entire 0.75-ha area sampled after the current monsoon yielded 429 seedlings < 16 cm, 126 seedlings > 16 cm in height, only 68 2nd-yr seedlings, and 2 3rd-yr seedlings. Sapling and tree diameters, ranked by size classes, confirm low regeneration (Fig. 4). Out of 328 individuals encountered in the 20 plots, we found only 10 (3%) saplings < 2 cm in diameter that were > 50 cm in height.

Mortality of *Trewia* in grassland latrines

Soon after fruit fall and manuring of seeds into latrines, two abundant species of hemipteran seed predators (*Macroceroea grandis* and *Iphita limbata* family: Largidae) attacked *Trewia* seeds. Adults of both species are strong fliers; these bugs found experimental

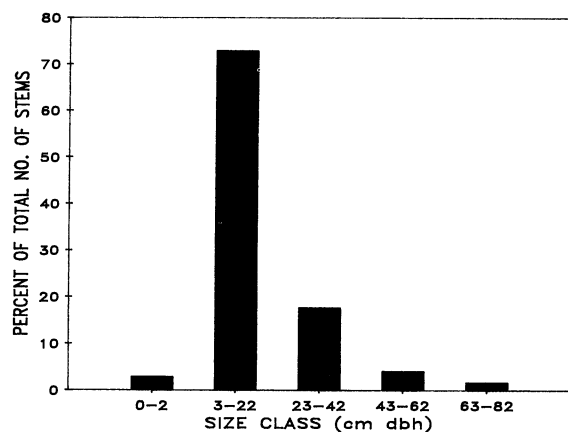


FIG. 4. Sapling and tree diameter at breast height (dbh) of *Trewia* germinated under the riverine forest canopy, ranked by size class.

grassland latrines deposited in tall grassland as far as 300 m beyond the forest edge within 2 d. Adults and juvenile forms were frequently observed climbing into rotting fruits to attack the seeds. Domestic cattle were the only mammalian herbivores of *Trewia* seedlings.

Because in grassland latrines most seeds that escaped seed predators germinated, intraspecific competition for light and nutrients in the rich dung there was probably intense. The seed load manured into one rhinoceros latrine exceeded 5600 intact seeds, and initial seedling density exceeded 15 seedlings/100 cm² (E. Dinerstein, *personal observation*). A small percentage of seedlings died from trampling when dominant males defecated and displayed at latrine sites, dragging their hooves through the dung.

Heavy floods during the monsoon, and fire during the hot season, emerged as the two most significant factors that altered the *Trewia* seed shadow created by rhinoceros in grasslands. In the monsoon of 1984, 500 marked seedlings that were scattered among 15 grassland latrines all died after a major flood buried them in a 50-cm layer of silt. Floods also washed *Trewia* seeds and fruits out of forest latrines and from the forest floor and onto the flood plain (E. Dinerstein, *personal observation*).

Fires set annually within the park by local grass cutters and by elephant drivers between January and May limited recruitment on grassland latrines. In 1985, experiments with an additional 500 marked seedlings divided among 15 grassland latrines revealed that mortality is 100% if a hot fire burns across a latrine. Saplings that were protected from fire for two growing seasons exceeded 2 m in height and survived grass fires if fires occurred either late in the afternoon or if fuel, in the form of dead grass around the saplings, was low.

DISCUSSION

Ingestion of Trewia by rhinoceros and colonization of the flood plain

With ≈ 60 rhinoceros in a 10.5-km² mix of flood plain and riverine forest, we estimated that our study population may have ingested 306 kg of fruit per day, and by the end of the monsoon may have manured at least 1.5×10^6 germinable seeds into grassland latrines within our study area. A single rhinoceros, with only 10% of its ingesta composed of *Trewia*, can still be carrying ≈ 10 kg of seeds and fruit tissues in its gut (probably > 1000 seeds/d). Furthermore, few contemporary frugivores can match rhinoceros in the quantity of seed-rich manure (up to 24.3 kg) produced in a single defecation. The heavy manure loads are significant because our experiments revealed that seeds defecated into latrines received a substantial boost from the manure in which they germinate and that seeds defecated in grassland latrines can grow to robust saplings after only two monsoons.

Aerial photographs of our study area in 1975 com-

pared with recent surveys attest to the rapid colonization of *Trewia* on Chitwan's flood plain. Verbal accounts of previous researchers (A. Laurie and J. L. D. Smith, *personal communication* and Smithsonian Institution/Nepal Terai Ecology Project (SI/NTEP) elephant drivers corroborate the observation of swift establishment of *Trewia*, particularly on rhinoceros latrines in grasslands. Fifteen years prior to our survey, much of the current study area was a major river course. The river then shifted, the exposed silt was colonized by grasses, and by 1986 small groves of *Trewia* dotted the flood plain, many of which contain active rhinoceros latrines. One of these areas, known locally as "Bhellurghari" ("Bhellur" being the local name for *Trewia nudiflora*) was 15 yr ago a series of rhinoceros latrines on the edge of a river terrace with many small seedlings and saplings emerging from the dung piles. A survey of *Trewia* in 1987 encountered 169 stems > 3 cm dbh. Mean (\pm SD) dbh for *Trewia* in this area was 33.4 ± 20.8 cm, and mean (\pm SD) height was 13.2 ± 6.5 m (range = 2.5–29.2 m), attesting to the fact that *Trewia* is one of the fastest growing tree species on the flood plain.

Plant fitness and dispersal of Trewia by rhinoceros

Despite the magnitude of the rhinoceros–*Trewia* interaction in Chitwan, frugivory remains nothing more than an interesting aspect of rhinoceros natural history unless it can be demonstrated that ingestion of *Trewia* by large mammals increases plant fitness. Our data demonstrate that from ingestion to seedling establishment on the flood plain, large mammals generate the demography and microgeography of the contemporary *Trewia* population. First, only large mammals disperse *Trewia* now. Because *Trewia* seeds are packed into a hard endocarp, seeds that are not freed from the fruit tissue through digestion by a large herbivore do not have a chance to germinate before the end of the monsoon (i.e., the optimal germination and growing season) (E. Dinerstein, *personal observation*). Second, despite the high density of *Trewia* in riverine forest and enormous fruit fall during the monsoon, the near absence of seedlings and saplings at the end of the wet season indicates that recruitment under the canopy is poor. In contemporary grasslands, high annual recruitment of *Trewia* may be a phenomenon associated with: (1) heavy rains during grass-cutting that preclude extensive burning (E. Dinerstein, *personal observation*), (2) light monsoons, or (3) when the monsoon fails entirely. Our observations suggest that recruitment under the canopy for this shade-intolerant, fast-growing species is determined by severe flooding, a phenomenon that opens up large patches of the forest and buries competing undergrowth in a layer of silt. Further research will determine if occasional premonsoon storms, which result in extensive windthrow, provide sufficient gaps

for recruitment to occur in the riverine forest (E. Dinerstein, *personal observation*).

The distribution of Trewia and rhinoceros

Assessing the influence of rhinoceros on the demography and distribution of *Trewia* requires study in areas where *Trewia* and flood plain grasslands occur but where rhinoceros have been extirpated. The evidence accumulated to date is mixed. Resident populations of rhinoceros disappeared from the Royal Bardia Reserve of Western Nepal over two centuries ago, and in this reserve *Trewia* is a rare to uncommon tree restricted to a few watercourses. No germination was observed in grasslands away from river banks even though axis deer, known *Trewia* eaters, are abundant in Bardia. Because flood plain dynamics are rapid in the Terai (Dinerstein 1987), we assume that if *Trewia* were effectively dispersed by other large wild herbivores, it would be more common than it is in Bardia. In a reserve in Bihar, India, *Trewia* flourishes in the absence of rhinoceros, but there it is dispersed by Indian bison, a wild cow (*Bos gaurus*) (B. Choudhury, *personal communication*). In Jaldhaphara Sanctuary, in West Bengal, where only a few rhinoceros remain, domestic buffalo disperse *Trewia* (L. Choudhury, *personal communication*). In another part of the Nepalese Terai and in northern India, *Trewia* is a common tree, but in the absence of wild herbivores, domestic cows disseminate *Trewia* fruits. After 13 rhinoceros were reintroduced into Bardia in 1986 (Mishra and Dinerstein 1987), preliminary data suggest that the recruitment of *Trewia* on grassland latrines has begun (G. Singh, *personal communication*).

Although rhinoceros figure prominently in the dispersal of *Trewia* and most probably in the evolution of fruit traits, it is unrealistic to expect that *Trewia* should disappear in the absence of rhinoceros. The absence of tight dependence of a given fruit on dispersal by a given frugivore may be attributed to: (1) the advantages for the plant to appeal to a wide spectrum of animals, (2) similar nutritional requirements among the fruit eaters, (3) opportunistic feeding by frugivores in search of an easy (undefended) meal, (4) the difficulty of evolving cues to limit detection and palatability for nontarget frugivores vs. target species, and (5) the loss of large frugivores over ecological and evolutionary time (Thompson 1982, Wheelwright and Orians 1982, Howe 1984). Nonetheless, megafauna-fruit interactions can be common in certain natural forests: Alexandré (1978), working in the Tal Forest, Ivory Coast, listed 30 species of trees and shrubs for which the African elephant seemed to be the only dispersal agent. Other such interactions between large indehiscent fruits and large terrestrial mammals probably await discovery in Southeast Asian tropical forests wherever such mammals are still common.

We believe that the most likely explanation for the occurrence of large indehiscent fruits in the Earth's woody flora is that these fruits, like *Trewia*, evolved in response to big herbivores. In Chitwan, woody plants producing such fruits constitute a relatively small proportion of the local flora. Nevertheless, the short species list, from a taxonomist's perspective, should not obscure its significance to the ecologist.

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