

Is Mora Taking Over? Testing the Limits to the Invasive Ability of *Mora excelsa* Benth. A Pilot Study.

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ABSTRACT

It is thought that the tropical tree *Mora excelsa* may be an invader of the high diversity Mixed Forest in Trinidad, reducing the diversity of the Mixed Forest, dominating the canopy and creating a stable Mora Forest type. A pilot transplant study was conducted in the Victoria-Mayaro Forest Reserve to assess if *Mora excelsa* seeds could survive post dispersal predation and germinate, and if the resulting seedlings could grow in a Mixed Forest adjacent to a Mora Forest. This would indicate if mora has the potential to expand beyond the current boundaries between the forest types.

The transplant experiment showed mora seeds could germinate in Mixed Forest albeit in half the numbers that they could in the Mora Forest. It also showed the mora seedlings could grow in the Mixed Forest. It was concluded that mora could potentially invade adjacent neighbouring Mixed Forest at least up to the seedling stage, and could expand the extent of the Mora Forest type.

INTRODUCTION

Mora Forests are different to the regular forests found in the tropics; they are dominated by a single species, *Mora excelsa* Benth., that can form up to 85-95% of the trees in the canopy (Beard 1946a). In most other tropical forests the frequency of the most dominant tree species in the canopy seldom rises above 10% of all trees. This mono-dominance phenomenon found in Mora Forests, and a few other tropical forests around the world, has intrigued foresters and plant ecologists (Beard 1946a, 1946b; Connell and Lowman 1989; Hart *et al.* 1989; Huston 1990; Richards 1996). The reasons for the dominance of mora are not known (Beard 1946a), however, the unusually high density of mora seedlings carpeting the ground of these forests is thought to be implicated (Beard 1946a; Janzen 1970). The density of mora seedlings can be as high as 50 seedlings per square metre (Oatham, unpublished data). The dense populations of these metre tall seedlings out-competes and excludes the seedlings of most other species (Rankin 1978; Oatham, unpublished data). Thus any regeneration of tree species after disturbance in the canopy is dominated by mora.

The dominance of *M. excelsa* is clearly evident in the field, making it easy to differentiate between Mora Forest and the neighbouring Mixed Forest. In addition, *M. excelsa* does not exist in a Mixed Forest at low den-

sities. Where it occurs it is dominant, where it is not dominant it is completely absent (Beard 1946a). Although *M. excelsa* is dominant in the Mora Forest, both in the canopy and in the seedling bank, the composition of the other tree species is identical to that in the neighbouring Mixed Forest (a more typical tropical forest) (Beard 1946a and b; Rankin 1978). This similarity and the inability of *Mora excelsa* to exist in low densities have led to speculation that mora is invading the surrounding Mixed Forest (Marshall 1934; Beard 1946a and b; Rankin 1978). Workers proposing the hypothesis point to the similarities in the tree community composition between Mora and Mixed Forests and the apparent phalanx-like advance of mora seedlings from the understory of the Mora Forest into the adjoining Mixed Forest (Marshall 1934; Beard 1946b; Rankin 1978; Richards 1996). They also use the apparent lack of relationship between the Mora-Mixed Forest boundary and edaphic features such as soil type and topography to support their claim (Beard 1946b; Rankin 1978; Richards 1996). It is not known if there are any biotic or abiotic restraints to the further expansion of the Mora Forest into the Mixed Forest. Few experimenters have tested this hypothesis, except for Rankin (1978). Rankin looked at the post dispersal predation and germination rates of a number of tree species, including mora, in the

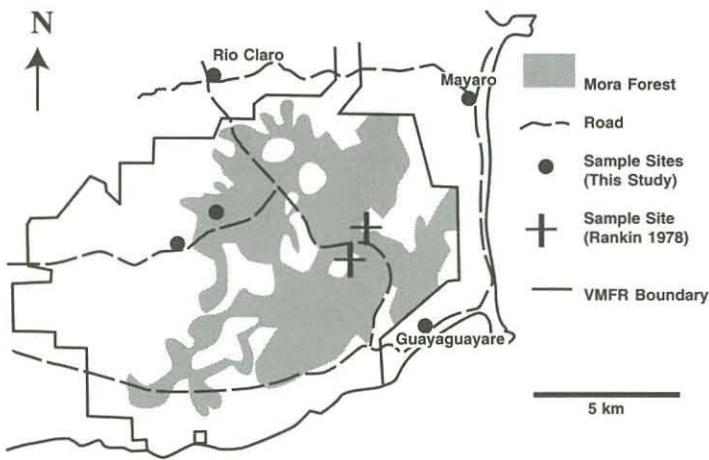


Figure 1. Location maps for sites used in this study and Rankin (1978) in the Victoria - Mayaro Forest Reserve.

Mora Forest, in the Mixed Forest and in the transition zone between them. She found that post-dispersal predation of mora seeds was higher in the Mixed Forest compared to the Mora Forest (19% seeds lost in the Mixed Forest and 1% of seeds lost in the Mora Forest). However, she hypothesized that the rate of seed predation of mora seeds and seedlings in the Mixed Forest, probably, was not a biotic block to mora invasion, as it would not be high enough to prevent the invasion of, and establishment in, the Mixed Forest. Rankin also compared the growth of mora seedlings in Mixed and Mora Forests and found no difference after 14 months, indicating no abiotic block to mora colonization of the Mixed Forest.

Rankin's study took place in the eastern part of the Victoria-Mayaro Forest Reserve (VMFR) (Fig. 1), where rainfall is relatively high (Rankin 1978). *M. excelsa* is known to be a water-loving tree (Ter Steege 1990, 1993a and b), so it is not known if her results can be translated several kilometers to the west, to the current distributional limits of Mora Forest in the VMFR (Fig. 1), which is an area with lower rainfall (Marshall 1934). It is not known how far west on a decreasing rainfall gradient Mora Forest will have the potential to actively colonize the Mixed Forest if it is truly acting as an invasive species.

The aim of the present pilot study was to test, on a small scale if the Mora Forest is at the western edge of its range in the VMFR or if it could potentially continue to invade the Mixed Forests further to the west. This was done by planting mora seeds in the Mixed Forest with the specific objectives of:

1. determining if a biotic block to expansion exists by comparing post-dispersal predation of

mora seeds in Mixed Forest with that in the Mora Forest at the edge of its distributional range in the VMFR;

2. determining if an abiotic block to expansion exists by comparing the growth of mora seedlings in Mixed Forest with that in Mora Forest over several months at the edge of its distributional range in the VMFR.

A more comprehensive study, with a greater number of replicates, was planned if the results from this pilot study were interesting.

SITE DESCRIPTION

This study was carried out in the Victoria-Mayaro Forest Reserve (VMFR) in south east Trinidad (Fig. 1). The site was chosen using the FRIM Forest Type and Inventory Map (FRIM 1980), as being at the western edge of the local range of Mora Forest in the VMFR.

Rainfall

The rainfall in the study area is 2300 to 2500mm per annum according to Marshall (1934). It decreases sharply from east to west, declining from nearly 3000 mm around Lizard Springs in the east to 2000mm along the Western boundary of the VMFR. The rainfall is mainly convectional, driven onshore by the prevailing NE Trade winds which also produce showers in the dry season. Only two to three months have rainfall less than 100mm in the eastern part of the VMFR (Beard 1946a). The showers do not penetrate very far inland so the western part of the reserve can suffer longer dry seasons with three to four months having rainfall less than 100mm.

Geology and Soils

Geology of the VMFR comprises mainly Upper Miocene sands, sandy shale with areas of Middle and Lower Miocene clays with sandy lenses (Marshall 1934). Recent alluvial deposits occur around the Ortoire and Poole Rivers. These run West to East across the North of the VMFR and around the Pilote and Moruga Rivers, draining the southern part of the Reserve. The soils of the area are clays and fine sandy clays on the intermediate uplands between the rivers and alluvial soils surrounding them (Ministry of Agriculture and the University of the West Indies 1971). The soils of the study area are Moruga Fine Sandy Clays, Ecclesville Clays and Saunders Road Clays. These soils have restricted internal drainage and are liable to water logging (Ministry

of Agriculture and the University of the West Indies 1971).

Vegetation Types

The vegetation types (Beard 1946b) of the area are the *Mora* and the *Carapa-Eschweilera-Sabal* faciations of the Lowland Seasonal Evergreen Forest Association. These are the Mora and Mixed Forest types mentioned in the introduction.

Human Influence

Human influence in the area of the study site is in the form of selective logging as the site is managed for timber production under the periodic block system (PBS) (Clubbe and Jhilmit 1992). When the transplant experiment was initiated, the last logging had occurred 25 years previously in the blocks where the quadrats were located. Old skid trails kept open by hunters were the only obvious sign of the previous logging event. Hunters make extensive use of the area which probably leads to a decline in the numbers of medium to large size vertebrates some of whom would be important seed or foliage predators. However, these animals, such as Red Brocket Deer, Agouti and Lappe, are still present in the area as evidenced by tracks observed during the study. Other smaller rodents such as Spiny Rats, Mice and Squirrels would be less affected by hunting and probably live at densities unaltered by humans.

METHODOLOGY

Site Selection

The sites were selected on the basis of a reported boundary between Mora Forest and Mixed Forest types. Once the general area of transition from one forest to the next was identified, a field survey was carried out to identify a specific location for the two sites, one in the Mora Forest and one in the Mixed Forest. The general location for each site was based on the following criteria:

- i) The site did not obviously show evidence of human disturbance.
- ii) The forest type was largely homogeneous.
- iii) The canopy was generally unbroken.
- iv) In the case of the Mixed Forest site, there was no Mora Forest west of it in the VMFR.

The quadrats in which the mora seeds were planted were located in the chosen area using randomly generated bearings and distances.

Seed Collection

During early January 2000 approximately 200 *Mora excelsa* seeds were collected in the general area of the study site. These were transported back to the laboratory where they were weighed and individually numbered using nail varnish. Seeds below 75g were discarded and 160 seeds were randomly selected from the remainder.

Seed Planting

Eighty seeds were planted in each forest type on the 9 January, 2000. Twenty seeds were planted in four quadrats in a 4 x 5 grid pattern with 30cm between each seed. The distance between seeds was selected based on the findings of Rankin (1978). She found that this spacing of seeds led to no adverse effect on seed and seedling performance due to intra-specific competition. The quadrats themselves were spaced out on a grid pattern with 20m between the quadrats. The seeds for each quadrat were randomly selected from the pool of seeds.

Periodic Measurements

Periodic measurements were made of seed/seedling mortality, seedling height, evidence of predation on the seed/cotyledons and evidence of herbivory damaging the leaves of seedlings. Timing of the measurements was determined by logistic constraints and measurements were made on days 25, 48, 91, and 191.

Analysis

The difference between the mortality and performance of the mora seeds and seedlings in the different forest types was examined using the following parameters:

- i) Seed and seedling mortalities.
- ii) Percentage seed germination.
- iii) Cotyledon damage.
- iv) Defoliation damage.
- v) Stems blown down.
- vi) Stems broken/bitten off.

The numbers of seeds or seedlings that showed damage in each of the above categories was compared between forest types by visual representation on a histogram showing the amount of damage at each measurement date. The average growth rate of seedlings in the two forest types was compared using a t-test. Growth rates were assessed between day 25 and 191, and between day 91 and 191. The two sets of growth rates were used to estimate the growth of the seedlings be-

cause it is likely the growth rates have different controls at different periods after germination. Mora seeds germinate and send up a shoot 50 to 150cm in height within the first 7 to 14 days. The height is attained without leaf expansion so it is probable that this initial growth spurt is due to the reserves in the large cotyledons of the seed. Abiotic conditions in the different forest types are unlikely to have an impact on this initial growth spurt which is more likely to be determined by the size of the seed. Therefore, to assess the effect of the abiotic conditions on growth rate in the different forest types, it was estimated between the last two measurement intervals to avoid initial growth spurts from germinating seeds. The growth rates were also compared from day 25 to day 191 to detect unexpected patterns in the initial growth after germination.

RESULTS

Seed Germination

Seed germination was identical in both forest types with 100 % germination being achieved in each by the 91st day (Fig 2A).

Cotyledon Damage

Damage to cotyledons of germinated or ungerminated seeds was much higher in the Mixed Forest compared to the Mora Forest (Fig. 2B). Over 50 % of seeds in the Mixed Forest (42 seeds) suffered some damage, but 3 % of seeds in the Mora Forest (2 seeds) were damaged. The majority of the damage to the cotyledons was incurred in the first 25 days after the seeds were planted.

Seed and Seedling Mortalities

Seed and seedling mortalities were far higher in the Mixed Forest quadrats compared to the Mora Forest (Fig 2C). In the Mixed Forest, 46 seeds or seedlings died (58 % mortality), the most dying between day 48 and day 91 (22 seeds/seedlings). In the Mora Forest 6 seeds/seedlings died (8 % mortality) with no particular interval seeing more mortalities.

Defoliation Damage

Defoliation of mora seedlings was restricted to the Mixed Forest type (Fig. 2D). Defoliation appeared to be mainly due to the activities of leaf-cutter ants (*Atta* sp.) and 34 individuals or 42 % of the mora seeds planted, were affected. Repeated defoliation of some individuals lead to their death but most individuals ap-

peared to suffer a single defoliation event and subsequently recovered.

Stems Blown Down

Seedlings affected toppled over without any damage to cotyledons, stem, root system or leaves. Usually the individuals that toppled over continued growing and re-established themselves without too much difficulty by branching upwards from existing leaf nodes. More seedlings toppled over in the Mora Forest type than in the Mixed Forest type (24 vs 7, Fig 2E). Most individuals toppled between days 25 and 48 after germination.

Stems Broken

Seedlings had their stems broken either by some agent pushing against them or by wind action. Many seedlings that broke appeared to be hollowed out at points on the stem which created a zone of weakness. Seedlings were also broken off by herbivores biting through the stem. More stems were broken in the Mixed Forest plots than in the Mora Forest plots (25 vs. 4, Fig. 2F). The majority of the damage occurred in the first 25 days while the shoots were emerging from the seed and had not yet fully expanded.

Growth of Mora Seedlings

Mora seedlings grew on average 33cm in the Mixed Forest plots and 37cm in the Mora Forest plots between days 25 and 191 (Table 1). The difference between the growth rates in the different forest types was not significant. Growth rates were also estimated for the period between the last two measurement intervals and gave an average growth of 2cm in the Mixed Forest and 1cm in the Mora Forest Type (Table 1). The difference in growth rates was not statistically significant.

Table 1. Average growth of *Mora excelsa* seedlings in Mora and Mixed Forests Measurements in cm. NS indicates no significant difference.

Average Growth between days 25 and 191				
	Mean	SD	n	T-test
Mixed	33	25	37	>0.05 (NS)
Mora	37	24	67	
Average Growth between days 91 and 191				
	Mean	SD	n	T-test
Mixed	2	5	37	>0.05 (NS)
Mora	1	5	67	

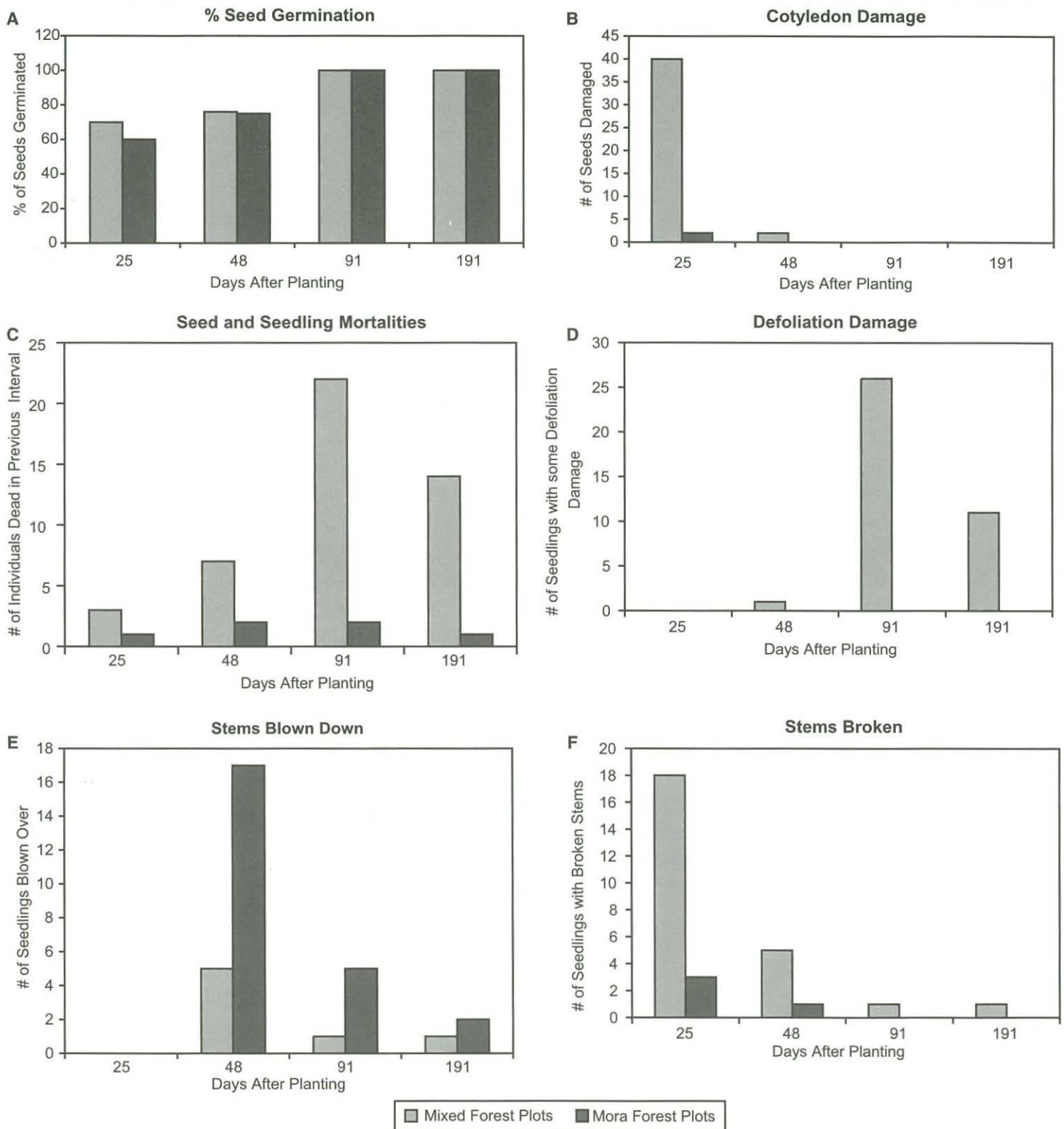


Fig. 2. Various statistics for the performance of *Mora excelsa* seeds and the resulting seedlings in Mora Forest and in Mixed Forest.

- A.** Percentage seed germination, the percentage of the 80 seeds planted in each forest that germinated.
- B.** Cotyledon damage, the number of seeds which showed evidence of being attacked by seed predators. No attempt is made to differentiate between the type of predators.
- C.** Mortalities of seeds and seedlings in each forest type as shown by the number of seeds lost in the preceding interval.
- D.** Defoliation Damage, the number of seedlings that have suffered defoliation of some degree by some herbivore (mainly leaf-cutter ants).
- E.** Stems blown down, the number of seedlings that have toppled over but are still alive with stem, cotyledons and roots all intact.
- F.** Stems Broken, the number of seedlings that have been snapped or bitten off. The seedling may or may not survive the attack.

DISCUSSION

The mora seeds and seedlings showed a much higher mortality rate in the Mixed Forest compared to the Mora Forest (58 % and 8 % mortality respectively). This confirms the findings of Rankin (1978) who also found this pattern although not as pronounced. The lack of replicates in this study makes it difficult to assess if the increased mortality in the Mixed Forest found in this study is ecologically significant.

The reason for the higher mortalities in the Mixed Forest plots appears to be biotic. The seedlings that died were subject to damage to the cotyledons (post-dispersal seed predation) or defoliation (leaf cutter ant herbivory) or broken/bitten off stems. Seedlings that died often suffered from a combination of all three. Rankin (1978) found low levels of post-dispersal seed predation in Mixed or Mora Forest primarily from mice (*Oryzomys* sp). The size of the incisor marks on the mora seeds in the Mixed Forest plots indicate mice were also responsible for mora seed predation in this study. Rankin (1978) did not find a significant difference in the numbers of seed attacks between the forest types. She also found deer were responsible for 39 % of attacks on mora seeds in the Mixed Forest. Deer ate the emerging shoot and often ripped the seed apart to get an ungerminated embryo. In this study it appears herbivores, possibly deer, bit off several of the seedlings in the Mixed Forest plot. Although each of the seed predator attacks taken by itself did not kill the mora seed or seedling outright, it weakened the seedling so that further damage was likely to be fatal. Mora seeds in the Mixed Forest that suffered only one of the above attacks managed to survive and in many cases thrive.

The absence in the Mora Forest plots of the levels of predation found in the Mixed Forest plots may be owing to seed predator satiation (Janzen 1970). The high densities of seeds found in a Mora Forest during the mass seed production of *Mora excelsa* would satiate a large community of predators especially if the seeds contain a low grade toxin. This would limit the number of seeds that a predator could eat (Janzen 1970). Rankin (1978) found such a toxin in her studies, a lactase specific lectin.

The susceptibility of mora seedlings to topple over in the Mora Forest plots was probably because of the deep leaf litter that is characteristic of Mora Forests (Rankin 1978; Oatham, unpublished data). This would hinder adequate rooting and the anchoring of the shoot during its early and rapid elongation. The ecological

significance of seedling toppling appears not to be great as the majority of seedlings which toppled survived and grew well.

It appears from the similarities of the growth rates of the mora seedlings in the Mora and the Mixed Forest plots that the biotic and abiotic conditions in the Mixed Forest do not prevent their growth and survival. Taking this into account, with the observation that 43 % of the mora seedlings survived to the end of this study, it appears that mora could potentially invade the Mixed Forest to the west of the current boundary between the two forest types. The survival of seedlings is of course only one stage through which mora must pass before it would reach maturity and truly come to dominate the forest. It remains to be seen if a 50 % loss of the seeds and seedlings dispersed into the Mixed Forest type would be enough to establish even a single mature individual after the attrition of the cohort as it grows to maturity. However, mortality is highest for tropical trees in the germination and seedling stages and decreases as the trees get bigger (Richards 1996).

The methodology used in this study would be appropriate to determine how far west in Trinidad mora seeds could establish and grow to dominate the forest. The aim of the authors is to carry out these further studies to determine the potential of the expansion of *M. excelsa*.

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