Regardless, regression models accounted for about half of the variance among populations. Although the unexplained variance could be random, it could also reflect adaptation of populations to environmental variables not considered in regression models. Because the present data constitute the genetics literature for western larch and because the data involve trees that were only 2 years old, there is little doubt that additional tests are needed to fully assess ecological adaptation within the species. Nevertheless, the observed patterns of variation are not only statistically detectable, but they are also clearly related to the environment. Therefore, until refined by additional tests, the present results are suitable for establishing breeding zones in tree improvement and for limiting seed transfer in artificial reforestation.

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Self Incompatibility in Gmelina arborea L. (Verbenaceae)

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Summary

G. arborea, a medium-sized to large tree native to the tropical forests of South and East Asia, is widely cultivated in tropical regions. Investigations of the pollination biology and the breeding system, conducted on trees cultivated in Costa Rica, reveal that the species is self-incompatible and pollinated by medium-sized to large bees. The abundant fruit set on Costa Rican trees suggest that the native bees are effective as pollination vectors for this species.

Key words: floral biology, pollination biology, apomixis, Costa Rica, pollen tube growth.

Zusammenfassung

Gmelina arborea L., ein mittelgroßer bis großer Baum, der in den tropischen Wäldern Süd- und Ostasiens natürlich vorkommt, wird in tropischen Regionen häufig kultiviert. Untersuchungen der Befruchtungsbiologie in Verbindung mit einem Züchtungsprogramm, die an Bäumen in Costa Rica durchgeführt wurden, zeigen, daß die Art selbstinkompatibel ist und von mittelgroßen bis großen Bienen bestäubt wird. Der reichliche Fruchtansatz der Bäume in Costa Rica macht deutlich, daß die einheimischen Bienen als Pollenüberträger für diese Art effektiv sind.

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Introduction

Gmelina arborea L. *(Verbenaceae)* is a medium-sized to large tree native to the deciduous and semi-deciduous forests of tropical South-east Asia (Troup, 1921; Lamb, 1968; Webb *et al.*, 1980). The species yields excellent timber that is used for a wide variety of purposes, including general light construction, fuel and charcoal, and building poles (Pearson and Brown, 1932; Lamb, 1968; Webb *et al.*, 1980). It is a fast growing plantation forestry species, and in recent years has emerged as a potentially important source of wood pulp (Doat, 1976). As a result, *G. arborea* plantations are being established throughout the old and new world tropics, and interest has developed to the point that the FAO Panel of Forest Gene Resources considers this species as one of top priority whose gene resources need exploration, utilization, and conservation (Greaves, 1977; Nas, 1980). Despite the considerable commercial potential of this species, not much is known about its reproductive biology, especially factors regulating the quality and quantity of seeds produced. Since most plant breeding involves the regulation of variation through control of the reproductive system, success in breeding programs is contingent upon knowledge concerning the reproductive biology of the spe-

cies involved. This paper reports the results of a study on the breeding system of *G. arborea*, and also presents some information on its floral and pollination biology.

Materials and Methods

The studies were conducted on six trees cultivated at Hacienda La Pacifica, Cañas, Guanacaste Province, Costa Rica. The surrounding vegetation is classified as lowland tropical semi-deciduous forest (HOLDRIDGE, *et al.*, 1971). The trees were planted as ornamentals in July, 1975, seeds having been obtained from the bulk collections of the Banco Latinamericano de Semillas Forestalles, CATIE, Turrialba, Costa Rica.

Controlled pollinations were performed from March 4 to March 10, 1981, to determine the extent of self-compatibility. The number of flowers pollinated ranged from 2 to 144 per tree. Since individual flowers usually opened before sunrise and were only receptive for 1 day, flower buds were isolated in Kraft paper bags (Pollen Tector #850; Carpenter Paper Company, Des Moines, Iowa) prior to the day of anthesis. Flowers were hand pollinated between 700 and 1200 hrs, and the bags were removed during the evening of the following day. A total of 199 flowers were self-pollinated and 206 cross-pollinated. In a test for apomixis, twenty-three flowers were emasculated and isolated for two days following the opening of flowers.

In order to examine pollen germination and pollen tube growth, 28 self-pollinated and 23 cross-pollinated flowers were fixed in FAA 12 hours after pollination. The styles and ovaries were cleared in 8N NaOH, prepared in aniline blue, and examined under a microscope illuminated with mercury vapor lamp and equipped with appropriate excitation and barrier filters (see MARTIN, 1959 for details about the preparation schedules).

The remaining 171 self-pollinated and 183 cross-pollinated flowers were censused periodically until the fruits matured; aborted fruits were collected and dissected to determine the extent of embryo development.

Results

Floral biology, pollination biology, and fruit set:

Observations on unbagged flowers showed that the relatively large, zygomorphic, perfect flowers open before sunrise, excrete more than 10ul of nectar, and are adapted for pollination by medium-sized to large bees. Stigmas were generally receptive from sunrise to 1300 hrs of the same day, during which time bees of the families *Anthophoridae* and *Xylocopidae* were observed visiting flowers. Fruit set, apparently from bee pollinations, was observed on each of the six trees included in this study. From 1 to 4 fruits developed from each inflorescence, with the number of inflorescences per tree ranging approximately from 30 to 350. It should be noted, however, that *G. arborea* is not native to Costa Rica, and observations were made on cultivated trees; the pollination biology of the species has not been studied in its native habitat, so comparable information is lacking.

Table 1. — Results of Controlled Pollinations

Tree Number	Number of hand-pollinated flowers maturing fruit (number in parenthesis indicate number of flowers pollinated)	
	Number of flowers selfed	Number of flowers crossed
1	0 (86)	39 (58)
2	0 (38)	31 (61)
3[1]	0 (1)	1 (1)
4[1]	0 (4)	8 (24)
5	0 (28)	27 (39)
6	0 (14)	0 (0)
Total	0 (171)	106 (183)

[1]) Tree used primarily as a pollen donor in cross-pollinations.

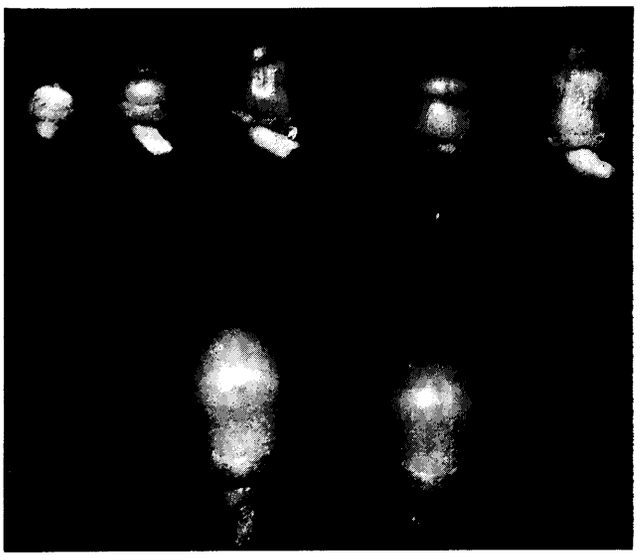

Figure 1. — Representative 10 day old self- (top) and cross-pollinations (bottom), enlarged 1.5 times. The figure illustrates the slower and more variable developmental rate of self-pollinaions.

Breeding system:

The results of controlled pollinations indicate that *G. arborea* is self-incompatible *(Table 1)*. Although none of the self-pollinated flowers developed into mature fruit, many such flowers did set fruits that developed to different sizes before their eventual abortion *(Figure 1)*. The maximum size reached by fruits resulting from selfed flowers was 1.6 by 0.7 cm, approximately 1/2 that of mature open- or cross-pollinated flowers. The maximum number of days of retention for fruit from a self-pollinated flower was 15. The fruit from cross-pollinations attained mature size in approximately 38 days.

The aborted fruits from the self-pollinated flowers were found to contain collapsed embryos (in the 4-locular ovary with one ovule in each locule, only one ovule usually developed into a seed).

The cytological examination of the stigmas and styles revealed no differences in pollen germination and pollen tube growth rates between selfed and cross-pollinated flowers. The selfed as well as cross-pollinated flowers showed pollen tubes traversing the length of the style and entering the ovary. The techniques employed did not reveal if the pollen tubes entered the ovules.

Ovaries from all flowers in the test for apomixis aborted within three days without any apparent sign of development.

Discussion

The results of this study indicate that *G. arborea* is self-incompatible. Self-incompatibility systems appear to be widespread among tropical forest trees (BAWA, 1974 and

1979). In *G. arborea* the system appears to operate after the zygote is formed. The evidence for the post-zygotic incompatibility system is based on: (a) collapsed embryos in fruits resulting from self-pollinated flowers, and (b) retention of fruits on self-pollinated flowers well beyond the time it takes the pollen tubes to reach ovules. One might argue that in the strict sense the system should be termed a self-sterility rather than a self-incompatibility system, but it should be noted that complex post-zygotic incompatibility systems involving pollen/ovule interactions are not unknown in angiosperms (DE NETTANCOURT, 1977), and appear to be quite common in tropical plants (BAWA, 1979).

Self-incompatibility has also been reported in teak (*Tectona grandis* L. f.), perhaps the only other tree species in the *Verbenaceae* for which information on the breeding system is available (HEDEGART, 1976). The extent of self-incompatibility was reported to vary from 96 to 100%, although no explanation was offered concerning how these numbers were obtained.

This self-incompatibility in *G. arborea* in part defines the options available in future breeding programs. For example, open-pollinated seed orchards designed to take advantage of the general combining ability of superior individuals can be established, without incurring the problems associated with selfing. Self-incompatibility also precludes the development of homozygous inbred lines, and subsequent formation of hybrid varieties.

A major concern in tropical forest tree-breeding is the extent to which specialized pollination systems can be manipulated when the species is cultivated far away from the range of its pollinators (BAWA, 1976). Although we have not compared the fruit set of *G. arborea* trees in Costa Rica with those that occur in the natural range of the species, apparently the bees of the Guanacaste region, at least, can serve as pollen vectors.

In short, *G. arborea* is self-incompatible but despite obligate outcrossing, changed pollination conditions are not detrimental to fruit set in Costa Rica.

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Effects of Inbreeding and Genetic Variances in a Natural Population of Tamarack (Larix laricina (Du Roi) K. Koch) in Eastern Canada

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Summary

A controlled pollination experiment in tamarack was done in four subpopulations of a natural stand in central New Brunswick, Canada, to define population structure. Estimates of relatedness among subpopulation trees were obtained by comparing self-pollination, neighbor, distant, long-distant, and unrelated polymix matings. The average relationship coefficient among neighbor (average 22 m between trees), distant (59 m), and long-distant (135 m) trees was found to be 0.167, 0.115, and 0.0, respectively. Self-pollination resulted in a significant reduction in seed set. Estimates of lethal equivalents for the selfed trees averaged 10.8 and ranged from 3.0 to 19.3. Relatively large specific combining ability variances were obtained for early seedling heights; however, interpretation and application of the variance components are complicated by the degree of relatedness among neighboring trees. Possible improvement procedures are discussed.

Key words: *L. laricina,* population structure, relationship, inbreeding, lethal equivalents, variance components, disconnected diallels and factorials.

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Zusammenfassung

Ein Versuch mit kontrollierter Bestäubung wurde bei vier Subpopulationen von *Larix laricina* (DU ROI) K. KOCH eines natürlichen Bestandes in Zentral-New Brunswick, Canada, durchgeführt, um die Populationsstruktur zu definieren. Schätzwerte für den Verwandschaftsgrad von Bäu-