Pollination in Bruguiera gymnorrhiza and Rhizophora mucronata (Rhizophoraceae) in Ishigaki Island, The Ryukyu Islands, Japan

Three genera and three species—Bruguiera gymnorrhiza (L.) Lamk., Kandelia candel (L.) Druce, and Rhizophora mucronata Lamk.—of mangrove Rhizophoraceae (tribe Rhizophoreae) occur naturally in the Ryukyu Islands and Southern Kyushu, Japan (Hou 1958, Walker 1976). In this locality these three taxa are at their northernmost geographic limit, but plants show no features of reproduction abnormal for the species, even though they are likely to be ecologically limited.

General comparative information regarding pollination ecology or floral biology of the mangrove Rhizophoraceae has been discussed by various workers (Guppy 1906, Gehrmann 1911, Doctors van Leeuwen 1927, Gill and Tomlinson 1969, Davey 1975, Tomlinson et al. 1979, Nakamura 1982, Tomlinson 1985). The Japanese mangrove species, however, are poorly documented in most standard references, especially with respect to pollination biology and breeding mechanisms. Recent field observations of B. gymnorrhiza and R. mucronata have clarified some of these reproductive features.

Field observations were made in November and December of 1984 in the mangrove forest of the Miyara River Biological Preserve, Ishigaki Island, the Ryukyu Islands, Japan, where B. gymnorrhiza and R. mucronata grow densely and vigorously together. Daily air temperature measured in the mangrove forest ranged from 18.5–28.5°C on average, whereas daily sea water temperature ranged from 18.5–25.0°C on average.

Two species of honeyeaters (Microscelis amaurotis stejnegeri Hartent and Zosterops palpebrosa yonakuni Kuroda) and a few insects (Camponotus sp. and Onychostylus pallidiolus Shiraki) were recorded feeding on the nectar of B. gymnorrhiza. Though the two bird species are migrants, during the period of observation at least two to four individuals of each species were observed continuously circulating within the mangrove forest and sometimes between neighboring mangrove forests. Pairs stay within a territory averaging 1400 m² during the breeding seasons (Haneda and Kobayashi 1967). Since access to nectar was only possible through the narrow opening between the independently closed petals, all large honeyeaters harvested nectar by perching or hanging from a branch near a pendulous flower. They probe upwards or at an angle through the central hole of petals to reach the nectar in the hypanthium cavity, which has an average capacity of 61.3 µl. Visits of M. amaurotis stejnegeri lasted 30–60 sec, whereas those of Z. palpebrosa yonakuni lasted 4–10 sec.

Floral expansion in B. gymnorrhiza occurs early in the morning and can be associated with an initial daily peak of bird visitation; more than 63 percent of the newly opened flowers opened their petals and released pollen by 9:15 A.M. In freshly opened flowers with untriggered petal pouches, insertion of a honeyeater’s bill into the hypanthium causes pollen to be released explosively as petals open and recurve instantly. This explosive method of pollen release in Bruguiera has been reported by Gehrmann (1911), Porsch (1924), Davey (1975), and Tomlinson et al. (1979). In contrast, small Camponotus sp. were probably too small to trigger pollen release and therefore cannot function as a pollen vector. O. pallidiolus visited at night when no pollen was available for dispersal.

Only 37.5 percent of the newly opened flowers of B. gymnorrhiza, which were observed before any bird visitation, showed 0.8–61.3 µl nectar in their hypanthia. However, the other 62.5 percent of the flowers showed no nectar secretion at the beginning of flowering and later began to produce nectar day by day. Some flowers continue to produce nectar continuously for a period of approximately one month after initial flower opening.

Twenty unfertilized flowers of B. gymnorrhiza, showing neither petal explosion nor nectar secretion at the beginning of flowering, and another 20 unfertilized flowers that contained 24–47 µl nectar 10 days after the beginning of flowering, were sampled and pollinated artificially with pollen obtained from a different tree of the species. They then seemed to stop secreting nectar. Any nectar accumulated before fertilization turned sour and later increased in viscosity since it was not foraged by birds. This observation suggests that pollination apparently inhibits nectar secretion and that discordant nectar secretion may have evolved to promote long periods of fertilization in the long, nonsynchronous flowering season and, subsequently, nonsynchronous maturity of fruits for long-term dispersal of seeds in unstable seashore environments.

Sugar concentration of the nectar of B. gymnorrhiza increases from 23 percent at the beginning of flowering to 37 percent three days later.

R. mucronata, sympatric with B. gymnorrhiza in the study site, attracted only a few small flower visitors, including Camponotus sp., O. pallidiolus, and a Collembola. It was not visited by nectarivorous birds. There is no hypanthium cavity, little nectar is produced, and there is no fragrance. Four to 12 sites on the short disc between the petal bases and the ovary secreted an average of 1.37 µl nectar per flower over a period of about four days. Sugar concentration of nectar is 12.9–16.9 percent. Flowering occurred in the afternoon, mostly between 3 and 5 p.m. The anthers began

to dehisce approximately one day before flowering and are fully dehisced when the flower starts to open. Pollen grains are often released within the flower bud, but some stay on the dehisced anthers for up to a few days until they are blown away. This phenomenon is common in most Rhizophora species, as noted by Guppy (1906), Gill and Tomlinson (1969), and Tomlinson et al. (1979).

The pollen grains of *Bruguiera gymnorrhiza* and *Rhizophora mucronata* are quite similar in morphology but differ in quantitative characters. They are tricolporate, elliptic in equatorial view, and circular in polar view. Pollen dimensions average 29.8 μm long and 17.2 μm diameter in *B. gymnorrhiza* and 24.2 μm long and 12.8 μm diameter in *R. mucronata*. They were never sticky, but rather very dry even at the beginning of flowering. Their surface sculpture is rather smooth, with numerous small and shallow depressions.

The stigma of *B. gymnorrhiza* is three lobed, whereas that of *R. mucronata* is two lobed, the lobes being small in both species. Each tip of the stigma of both species contains small papilla and secretes mucilage, which retains pollen readily.
TABLE 1. Artificial crosses attempted in B. gymnorrhiza and R. mucronata in Miyara River, Ishigaki Island.

<table>
<thead>
<tr>
<th>Type of fertilization</th>
<th>Bruguiera gymnorrhiza</th>
<th>Rhizophora mucronata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apomixis:</td>
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<td></td>
</tr>
<tr>
<td>No. of flowers tested</td>
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<td>20</td>
</tr>
<tr>
<td>Fertilized</td>
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<td>0</td>
</tr>
<tr>
<td>Nonfertilized</td>
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<td>20</td>
</tr>
<tr>
<td>Autogamy:</td>
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<td></td>
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<td>No. of flowers tested</td>
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<td>20</td>
</tr>
<tr>
<td>Fertilized</td>
<td>12</td>
<td>19</td>
</tr>
<tr>
<td>Failure</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Geitonogamy:</td>
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<td>40</td>
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<tr>
<td>Fertilized</td>
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<td>36</td>
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<tr>
<td>Failure</td>
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<td>4</td>
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<tr>
<td>Allogamy:</td>
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<td>No. of flowers tested</td>
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<td>41</td>
</tr>
<tr>
<td>Fertilized</td>
<td>38</td>
<td>12</td>
</tr>
<tr>
<td>Failure</td>
<td>2</td>
<td>29</td>
</tr>
</tbody>
</table>

Hand pollinations demonstrated that both B. gymnorrhiza and R. mucronata can be fertilized under conditions of allogamy, autogamy, and geitonogamy (Table 1).

These comparative observations lead to the conclusion that B. gymnorrhiza is exclusively pollinated by birds, and R. mucronata is wind pollinated perhaps with some pollination by small insects. From this we infer that long-distance outcrossing and heterozygosity have been favored for B. gymnorrhiza, whereas short-distance outcrossing is favored for R. mucronata. Indeed, flowers of R. mucronata have a greater morphological variability than those of B. gymnorrhiza (Masuda and Nakamura 1985, Nakamura et al. 1985), presumably because of decreased selection pressure from pollinators.

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