The Search for Self-Incompatible *L. Leucocephala*: Theoretical Considerations

*Leucaena leucocephala*, a polyploid with $2n = 104$, is highly self-compatible (SC) or "self-fertile". No systematic search has been conducted for self-incompatible (SI) or "self-sterile" trees (with full gamete fertility) in this species. However, SI trees are fully to be expected and to have potential economic value.

Diploid *L. diversifolia* and other diploid (2n=52 or =56) *L. Spp.* have been shown to be self-incompatible by Pan (1985), who further identified the controlling S locus. The locus is of the gametophytic type characteristic of legumes and other flowering plants with binucleate pollen (Brewbaker, 1967). It can thus be inferred that *L. leucocephala*, a functional tetraploid, is self-compatible (SC) or "self-fertile" by virtue of the classic reversion of SI to SC that can occur in tetraploids (Brewbaker, 1953, 1954). The breakdown affects only certain genotypes, leaving the option for segregation of SI plants. Other tetraploids in the genus *Leucaena* include *L. diversifolia* (Schlecht.) Benth. subsp. *diversifolia*, 2n = 104 and SC, and *L. pallida* Britton & Rose, 2n = 104 and SI, illustrating differences within this genus.

Theoretical considerations of this phenomenon are given here, following a discussion of the value of the search for SI plants in this species.

**Potential value of SI *L. leucocephala* trees.** Self-incompatibility has long been exploited in the production of hybrid seeds through methods that permit temporary inbreeding and production of homozygous lines, e.g., in cabbage and its relatives. SI can also be exploited to produce seedless lines through cloning of a single plant, making a population that is SI and cross-sterile; a classic example is the cultivated pineapple. Clones of SI plants of *L. leucocephala* could be paired for hybrid seed production, used for interspecific crosses, or mixed to exploit the heterosis of synthetics. This presupposes that yield heterosis does exist, a reasonable assumption based on the evolution of SC species that show yield heterosis (e.g., commercial tomato) from SI relatives.

Some of the most valuable genetic variation to improve commercial leucaenas—e.g., tolerance to acidity, cold, psyllids—occurs in other *Leucaena species*. Sorensson (unpublished) has shown that *L. leucocephala* can be used as female parent in fertile crosses to all 10 species tested. Some of these hybrids are of immediate potential commercial interest, such as *L. leucocephala* x *L. diversifolia* (4N), e.g., K8 x K156. Hybrid seeds of such crosses could be produced economically in isolation on SI trees cloned as female parents for the cross.

Seedlessness itself is surely desirable in some uses of leucaena. Improved wood yields in plantations may even be predicted, since pod and seed formation are major drains on fixed carbon.

**Theoretical considerations in the search for SI trees.** Induced polyploids in SI legumes like alsike clover (Brewbaker, 1953, 1958) revealed that only 5 to 10 percent of the original polyploids were SC. Later generations of tetraploid alsike popu-
lations, in contrast, ranged from 39 to 84% SC as a result of genetic recombinations and selective advantage of SC pollen. We showed that these phenomena were based on interaction ("competition") of S alleles in selected heterogenic (heterozygous) pollen grains. In SC tetraploids of the diallelic genotype S2S2S3S3, for example, the pollen are of 3 genotypes—S2S2, S2S3, and S3S3. These are shed in ratios ranging from 1:4:1 to 3:8:3, depending on position of the S gene relative to the centromere (Brewbaker, 1955). Self-compatibility results only from the function of the heterogenic (e.g., S2S3) pollen, a phenomenon now validated in many species.

Essentially all seeds of *L. leucocephala* appear to be derived by selfing, and all trees from selfs will be diallelic for S alleles. Depending on the origin of a polyploid species, it may have few to many such S alleles. If based on a single chromosome doubling event of a diploid such as S2S3, all trees could be S2S2S3S3, or variations thereof. It is more likely, however, that *L. leucocephala* is an amphiploid with a great many S alleles (minimally, 4).

A significant feature of this theory is that all selfed progeny of SC plants will be SC, since all will obtain both alleles that show the "competition interaction" of the parent tree. A search for SI trees of leucaena among normal selfed progenies is therefore doomed to failure.

When two SC trees are hybridized in S allele tetraploids, however, it is possible to obtain SI plants, as shown for induced polyploid clovers (Brewbaker, 1954, 1955). Theoretical considerations are summarized below; alleles are simply designated by numbers, e.g., 2 = S2, 4 = S4, etc.

Assume a cross of two SC trees, genotypes 1122 x 3344
Assume 12 and 34 are "competition male gametes" causing SC

Progeny, using Punnett square, have frequencies in parentheses:

<table>
<thead>
<tr>
<th>Female Gametes</th>
<th>Male Gametes</th>
<th>SI:SC Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1/6) 11</td>
<td>(1/36) 1133</td>
<td>11:25</td>
</tr>
<tr>
<td>(4/6) 12</td>
<td>(4/36) 1233</td>
<td>6:30</td>
</tr>
<tr>
<td>(1/6) 22</td>
<td>(1/36) 2233</td>
<td>1:35</td>
</tr>
</tbody>
</table>

Expected frequencies of SI and SF plants arising from this cross are as follows:

<table>
<thead>
<tr>
<th>Competition gametes</th>
<th>SI:SC Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) One of the 4, e.g. 13</td>
<td>11:25</td>
</tr>
<tr>
<td>(b) Two of the 4, e.g. 13, 14</td>
<td>6:30</td>
</tr>
<tr>
<td>(c) Three of the 4, e.g. 13, 14, 23</td>
<td>1:35</td>
</tr>
<tr>
<td>(d) All of the 4, e.g. 13, 14, 23, 24</td>
<td>0:1</td>
</tr>
</tbody>
</table>

The frequencies given above are for chromosome-assortment ratios, where S locus is assumed to be very close to the centromere. At greater distances from the centromere, these ratios change...
slightly; e.g., for the case of (a) above, expected ratio will be between 11 SI:25 SC and 75 SI: 121 SC (or between 69 and 62 percent SC, resp.).

Previous clover work showed that SC gametic combinations may be expected to increase but never totally dominate populations of newly-derived tetraploids from SI diploids, and that seed sets upon selfing would increase gradually as SC dominated the population. It seems reasonable to expect the frequency of SC gametes in L. leucocephala to be 50% or less. At a frequency of 50%, most crosses of genetically different varieties (e.g., 1122 x 3344, or 1122 x 1133, etc.) would therefore be expected to segregate SI trees.

Expected appearance of SI trees. The diploid species of Leucaena are SI, and in our nurseries they usually set seed well by natural crossing. However, seed sets of SI trees are often distinct from those of the self-fertilizing ones. SI trees tend to produce few pods per head, indicating random insect-pollinator effectiveness, and to flower for longer periods of time. In contrast, SC L. leucocephala plants tend to produce heavy pod sets simultaneously, cycling in and out of flowering. Although such empirical studies of phenology may be useful guides, bagging or hand-pollinating is preferred. Many L. leucocephala heads set one or more pods when covered with bags and not manipulated. Better still is to cover a head, return in late anthesis and self-pollinate. In isolation, naturally, a single self-sterile tree would be seedless.

References: