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# Annual Fertility Variation in Clonal Seed Orchards of Teak (*Tectona grandis* L.f.) and its Impact on Seed Crop

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**Abstract**

Fertility variation was studied in two clonal seed orchards (CSO) of teak in four consecutive years (2003–2006). Both orchards were raised in 1976 with grafts of phenotypes selected for growth and form. The seed orchards of CSO I (Topslip, Tamil Nadu State) and CSO II (Walayar, Kerala State) have 15 and 20 clones, respectively, with 13 common clones. The proportion of flowering ramets was generally low ranging from 16 to 53% across years. The best fruit yield during the study period was around 18 kg ha$^{-1}$ in CSO I and 17 kg ha$^{-1}$ in CSO II. Highly significant clonal variation and clone by year and clone by site interactions were observed for fertility traits. The clonal contribution was more skewed in poor flowering years than in abundant flowering years and in CSO II than in CSO I. Broad sense heritability for flower and fruit production per tree was low to moderate (0.16 to 0.55). Flower and fruit production by individual ramets in successive years were positively correlated. Correlations between reproductive and growth traits were generally low, but correlation was strong between flowering and fruiting. Fertility variation and group coancestry were higher in poor flowering years than in abundant years and in CSO II than CSO I. Restricting seed collection to abundant flowering years, adjusting ramet number to balance contribution of clones and mixing of seeds from successive years are suggested to reduce relatedness among orchard progeny. The usefulness of low input breeding options for teak like seed production areas are also discussed.

*Key words:* Flowering, fruit production, diversity, coancestry, heritability, status number.

## Introduction

Teak (*Tectona grandis* L.f.) is a high value tropical species acclaimed world over for its timber quality. Increased demand for timber and restrictions on felling from natural forests has prompted large scale planting of teak throughout the tropics (PANDEY and BROWN, 2000). Large quantities of seed are required every year to establish new plantations. Clonal seed orchards (CSO) were planted in India and other countries for domesticating and breeding teak and produce geneticalally improved seed. The first seed orchard was established in India during 1962 and since then more than 1000 ha of CSOs have been planted in different parts of the country (KEDHARNATH and MATTHEWS, 1962; KATWAL, 2005). Seed production and germination has been generally low in most of these orchards (INDIRA and BASHA, 1999; KJÆR *et al.,* 1999; MATHEW and VASUDEVA, 2003). As a result, seed requirement for new plantations is met from seed production areas and existing plantations. Teak breeding programmes have not moved beyond the first generation clonal orchards.

Low seed production in teak orchards has prompted many studies on the reproductive behaviour of teak dur-

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ing the past decade (KERTADIKARA and PRAT, 1995; KJÆR and SUANGTHO, 1995; NAGARAJAN *et al.,* 1996; PALUPI and OWENS, 1998; GUNAGA and VASUDEVA, 2002; VARGHESE *et al.,* 2005). Absence of flowering, asynchrony in flowering phenology among clones, pollinator limitation and low levels of cross pollination were reported as major reasons for low output in seed orchards.

The objectives of the present study were: to quantify flower and fruit production in two CSOs during consecutive years, to estimate fertility variation and its effect on orchard seed crops and to determine factors that influence fertility status of orchards.

## Materials and Methods

*Seed orchard details*

The present study was conducted in two CSOs of teak located in South India: CSO I is located at Topslip in Tamil Nadu State (10° 25' N, 76° 50' E; rainfall: 1348 mm) with 15 clones selected from the Western Ghats region in the States of Tamil Nadu (TN clones) and Kerala (KL clones) (latitudes 10 to 11° N). CSO II located at Walayar in Kerala State (10° 50' N; 76° 50' E; rainfall: 1229 mm) has 20 clones of which 19 are from Western Ghats region. One clone (SBL) is from the Eastern Ghats region (17° 40' N; 81° 00' E; rainfall: 1000 mm) of Andhra Pradesh State. The two orchards together have 22 clones of which 13 are common between them.

The CSOs were established by planting grafts of plus trees selected from natural forests and plantations mostly on the basis of superior growth and form. These plus trees were at least 50 years old at the time of selection and grafting. Both the orchards were established in the year 1976 in a completely randomized design at a spacing of 5 m. Two thinnings were undertaken in the orchards to maintain an average spacing of about 10 m between trees for crown development and flower production. At the time of the study CSO I had 175 ramets comprising 6 to 19 ramets each of the 15 clones and CSO II had 454 ramets represented by 13 to 30 trees each of 20 clones. In 2006 the height of trees in CSO I ranged from 15 to 27 m (mean = 23 m) and diameter from 28 to 56 cm (mean = 38 cm) while trees were 11 to 25 m (mean = 17 m) tall and the diameter was from 15 to 53 cm (mean = 32 m) in CSO II.

*Estimation of flower and fruit production*

Flowering and fruiting were assessed during four consecutive years from 2003 to 2006. All the ramets in the orchards were assessed for flower and fruit production following the methods of BILA *et al.* (1999). Diameter was measured for all trees every year while total height and clear bole height were measured only in the last year *i.e.* 2006. The significance of clonal variation for different traits was determined through analysis of variance. The orchards were divided into 7 blocks and one random flowering tree per clone in each block was chosen for the analysis. Flower and fruit count data were square root transformed before analyzing. Broad sense heritabilities on individual ramet basis were calculated for all traits using the formula [1] (MATZIRIS, 1993).

$$H^2 = \sigma^2_c / \sigma^2_c + \sigma^2_e \quad [1]$$

Where $H^2$ is the broad sense heritability, $\sigma^2_c$ and $\sigma^2_e$ are variance components for clones and residual respectively. Trait-trait and age-age simple correlations were calculated.

The male and female fertility of a tree was considered to be proportional to the number of male and female gametes produced by the tree (GREGORIUS, 1989). Gender fertilities were assumed to be equal to the number of reproductive structures (flowers and fruits) expressed as a proportion of all trees. Total fertility of a tree ($p_i$) was taken as the average of the male ($m_i$) and female ($f_i$) fertilities of each tree.

*Fertility variation*

The measures used are applicable to an assumed gene pool or seed orchard crop where clones contribute proportional to their assumed fertility in the seed orchard. Sibling coefficient ($\Psi$) is the probability that two genes randomly drawn from the gamete gene pool originate from the same parent compared to the probability if the parents had equal representation (KANG and LINDGREN, 1999). It is used to describe fertility variation among the trees and calculated from the number of trees evaluated ($N$) and individual fertility ($p_i$) of each tree.

$$\psi = N\sum_{i=1}^{N} p_i^2 \quad [2]$$

A maternal (female) sibling coefficient ($\Psi_f$) and a paternal (male) sibling coefficient ($\Psi_m$) can be given

$$\psi_f = N\sum_{i=1}^{N} f_i^2 \quad [3]$$

$$\psi_m = N\sum_{i=1}^{N} m_i^2 \quad [4]$$

*Coancestry, effective population size and status number*

Group coancestry ($\Theta$) is the probability that two genes chosen at random from a gene pool are identical by descent (COCKERHAM, 1967). If the trees are non related and non-inbred, all pair coancestries are equal to zero and all self coancestries are equal to 0.5 and the group coancestry was calculated using the methods from LINDGREN and MULLIN (1998).

$$\Theta = 0.5\sum_{i=1}^{N} p_i^2 \quad [5]$$

The group coancestry can be calculated considering male ($mi$) and female fertilities ($fi$) as

$$\Theta = 0.5\sum_{i=1}^{N}\left(\frac{m_i + f_i}{2}\right)^2 \quad [6]$$

The status number ($Ns$, which can be considered as an effective population number) is the number of genotypes sampled from the reference population that would cause the same deviation in gene frequencies as in the studied population (LINDGREN and MULLIN, 1998) ($Ns = 0.5/\Theta$).



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The relative status number of clones (*Nr*) can be used to relate the status number to the actual number of clones in the orchard.

$$N_r = \frac{N_s}{N} \quad [7]$$

*Gene diversity*

Expected relative gene diversity (GD) is a function of the group coancestry and can be calculated in the orchard relative to a reference population. The reference population, which is the natural forest that the plus trees were selected from, is considered to have very low group coancestry as it is considered to have infinite number of unrelated individuals. Though it may not be true in the strict sense, the assumption of initial zero coancestry can be seen as fixing a reference point against which later coancestry changes are referred to rather than that trees are unrelated (LINDGREN and KANG, 1997; KANG and LINDGREN, 1999).

$$GD = 1 - \Theta \quad [8]$$

Group coancestry can be seen as the fraction of gene diversity lost since tree breeding was initiated.

## Results

*Annual variation in flowering*

Large year-to-year variation in flowering was observed in both the orchards (*Table 1*). ANOVA showed highly significant ($p < 0.01$) clone by year interaction for flowering and fruiting traits (*Table 2*). The proportion of flowering ramets in different years ranged from 16 to 52.6% and each orchard had a single abundant flowering year. About 45% of trees in CSO I flowered during 2005 with an average of 36900 flowers per tree. Fruitset and fruits per tree were also the highest in that year resulting in the maximum fruit production of 17.8 kg ha$^{-1}$ (*Table 1*). Although 52.6% of trees flowered in 2003, flowers per tree and fruitset were lower than 2005 resulting in production of only 2.7 kg fruits ha$^{-1}$. In CSO II, the highest proportion of flowering trees was in 2006 (38.9%) with 16.7 kg of fruits per ha. In the rest of the years, the proportion of flowering trees ranged from 16.7 to 27.7% and fruit production from 8.7 to 11.1 kg ha$^{-1}$. Fruitset was less than 1% in all years and higher in CSO II than CSO I except in 2005. In general fruit production was found to be a function of number of trees flowering and the extent of fruitset in an orchard.

Clones and ramets of a clone were not consistent in fertility and reproductive output across years. Only 60% of clones flowered in all four years in both the orchards. No clear flowering pattern was discernible among rest of the clones but a few showed tendency towards abundant flowering in alternate years. At individual ramet level, about one third in CSO I and half in CSO II did not flower in any of the four years. Only 11% of ramets in CSO I and 19.8% in CSO II flowered consecutively for four years.

*Clonal variation in flowering abundance*

Significant variation ($P < 0.05$) was found for flower and fruit production and fruit set among clones in each year. A few clones always contributed considerably more than others. This imbalance was higher in CSO II than in CSO I and during low flowering years than abundant flowering years (*Fig. 1*). In CSO I about 80% of flowers were contributed by 50% of the clones in 2003, 2005 and 2006 but the same pattern for fruit production was observed only in 2005. In CSO II, 40% of clones con-

*Table 1.* – Flowering and fruiting in two teak CSOs for four consecutive years.

| Character | | Topslip[1] | | | | Walayar[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 2003 | 2004 | 2005 | 2006 | 2003 | 2004 | 2005 | 2006 |
| Clones with flowers | | 15 | 10 | 15 | 13 | 13 | 17 | 17 | 18 |
| Proportion of flowering trees (%) | | 52.6 | 16 | 44.6 | 21.7 | 23.1 | 16.7 | 27.7 | 38.9 |
| Flowers per tree (x1000) | Min. | 0.8 | 2.3 | 0.7 | 2.7 | 4.0 | 2.4 | 2.5 | 2.7 |
| | Max. | 257.9 | 114.2 | 273.8 | 43.9 | 496.1 | 555.6 | 477.9 | 345 |
| | Mean | 26.2 | 23.9 | 36.9 | 18.2 | 85.0 | 80.3 | 57.2 | 63.6 |
| Fruits per tree | Min. | 0 | 18 | 3 | 0 | 3 | 1 | 5 | 15 |
| | Max. | 780 | 528 | 1667 | 250 | 8010 | 7070 | 3720 | 3142 |
| | Mean | 19 | 96 | 298 | 54 | 532 | 671 | 485 | 471 |
| Fruit set per tree (%) | Min. | 0 | 0 | 0.08 | 0 | 0.00 | 0.02 | 0.04 | 0.13 |
| | Max. | 2.96 | 0.77 | 2.74 | 0.88 | 2.68 | 3.65 | 2.66 | 2.35 |
| | Mean | 0.17 | 0.24 | 0.81 | 0.24 | 0.48 | 0.75 | 0.67 | 0.74 |
| Total fruit production (kg)* | | 1.7 | 0.7 | 11.2 | 1.0 | 21.8 | 23.5 | 27.6 | 41.7 |
| Fruit production per hectare of orchard (kg) | | 2.7 | 1.1 | 17.8 | 1.6 | 8.7 | 9.4 | 11.1 | 16.7 |

[1] CSO I (clones: 15; ramets: 175); [2] CSO II (clones: 20; ramets: 454).
* assuming 2000 fruits per kg.



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*Table 2.* – Means squares (MS) and their significance (P) from ANOVA for clone x year and clone x site for flower and fruit production in two teak orchards.

| Source of variation | Flowers | | | Fruits | |
|---|---|---|---|---|---|
| | df | MS | P | MS | P |
| **Topslip** | | | | | |
| Year | 3 | 23793.30 | 0.002 | 225.20 | 0.000 |
| Clone | 14 | 5000.13 | 0.361 | 16.01 | 0.247 |
| Clone x year | 42 | 1302.80 | 0.012 | 8.39 | 0.000 |
| Pooled residual | 336 | 806.84 | | 4.01 | |
| **Walayar** | | | | | |
| Year | 3 | 8065.78 | 0.315 | 23908.83 | 0.009 |
| Clone | 19 | 17032.55 | 0.001 | 2957.35 | 0.202 |
| Clone x year | 57 | 4581.57 | 0.000 | 2354.53 | 0.000 |
| Pooled residual | 456 | 1592.64 | | 232.58 | |
| **Across locations** | | | | | |
| Site | 1 | 2858.30 | 0.452 | 169.73 | 0.139 |
| Clone | 12 | 3970.74 | 0.628 | 35.58 | 0.370 |
| Clone x site | 12 | 2286.43 | 0.000 | 28.33 | 0.000 |
| Pooled residual | 144 | 569.14 | | 6.94 | |

tributed 80% of the flower and seed produced even in the abundant flowering year (2006). Contribution of clones was highly skewed in the poor flowering year, 2004 in which a single clone (SBL 1) produced 55% of flowers and 50% of fruits in CSO II. There was a large ramet-to-ramet variation in flowering and fruiting abundance within a clone. Number of flowering ramets per clone ranged from 1 to 32. The flowers produced per tree ranged from 700 to 555,600 and fruits from 1 to 8010 (*Table 1*). Clone differences significantly consistent over the years were found for flowers but not for fruits (*Table 2*).

Fertility of clones differed between the two orchards. ANOVA showed highly significant ($p < 0.001$) clone by site interaction for flowering and fruiting traits (*Table 2*), thus clone differences may not be general over all sites, but different on different sites. In CSO II clones KLS3 and KLS4 showed no flowering in all 4 years but were among the most fertile clones in all years in CSO I. KLS1 and KLS2 were shy flowerers in CSO II but flowered better in CSO I. A few other clones had consistent poor or high fertility across orchards.

Broad sense heritability ($H^2$) varied across years and locations for growth and fertility traits (*Table 3*). Heritability for fertility traits was generally higher in CSO II and in poor flowering years. The average heritability for diameter and fruits per tree was low and moderate for flowers per tree and fruitset. There was a strong and positive correlation between flower and fruit production in all the years in both orchards (*Table 4*). But fruitset more strongly correlated with fruits per tree than flowers per tree. While diameter showed a weak positive correlation with fertility traits, total height, clear bole height, and height to clear bole ratio had a weakly negative correlation with fertility traits,

In CSO II, the most fertile clone SBL 1 had the lowest height to bole length ratio of 0.46 while the rest of the clones had a ratio of >0.6. At individual ramet level, correlation between flower production in successive years was positive and significant. Correlation between fruits per tree in successive years was generally positive and significant (except between 2003 and 2004 in CSO I which was weakly negative) (*Table 5*).

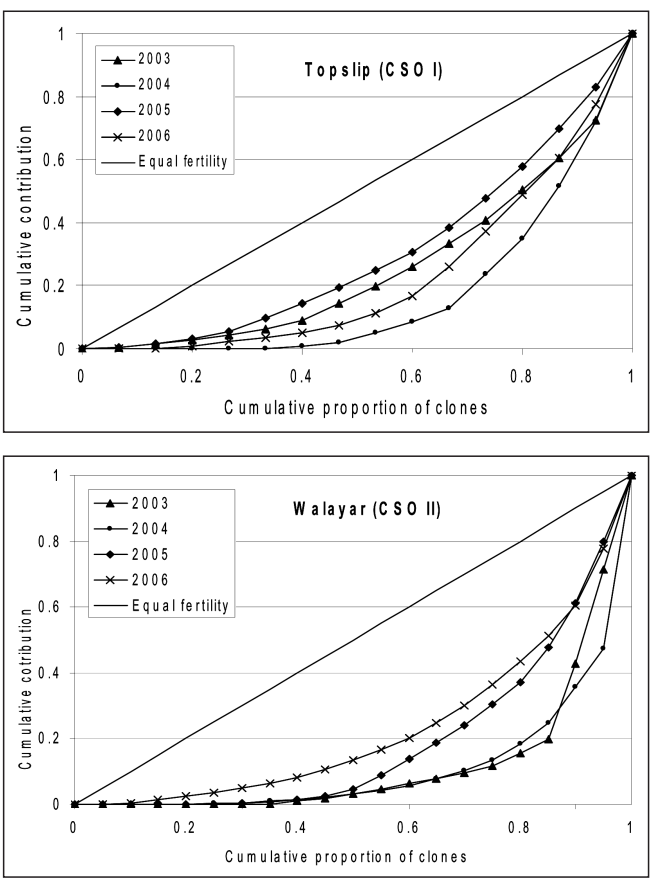


*Figure 1.* – Cumulative contribution of gametes by teak clones in two orchards for four years.



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*Table 3.* – Broad sense heritability ($H^2$) values for DBH and reproductive traits in two clonal seed orchards of teak.

| Trait | Broad sense heritability ($H^2$) | | | | | |
|---|---|---|---|---|---|---|
| | 2003 | 2004 | 2005 | 2006 | Mean | SD |
| Topslip (CSO I) | | | | | | |
| DBH | 0.364 | 0.129 | 0.211 | 0.513 | 0.304 | 0.170 |
| Flowers | 0.348 | 0.310 | 0.263 | 0.755 | 0.419 | 0.227 |
| Fruits | 0.075 | NC | 0.142 | 0.272 | 0.163 | 0.100 |
| Fruitset | 0.043 | NC | 0.692 | 0.514 | 0.417 | 0.335 |
| Walayar (CSO II) | | | | | | |
| DBH | 0.369 | 0.291 | 0.245 | 0.145 | 0.263 | 0.094 |
| Flowers | 0.762 | 0.591 | 0.298 | 0.570 | 0.555 | 0.192 |
| Fruits | 0.283 | 0.292 | 0.200 | 0.354 | 0.282 | 0.064 |
| Fruitset | 0.479 | 0.361 | 0.460 | 0.477 | 0.444 | 0.056 |

NC – not calculated.

*Table 4.* – Correlation between flowering and fruit production and growth and form traits.

| | Topslip (CSO I) | | | | Walayar (CSO II) | | | |
|---|---|---|---|---|---|---|---|---|
| | 2003 | 2004 | 2005 | 2006 | 2003 | 2004 | 2005 | 2006 |
| Flowers per tree with | | | | | | | | |
| Height | 0.084 | -0.040 | 0.090 | 0.573** | -0.019 | -0.065 | 0.053 | 0.048 |
| Clear bole height | 0.008 | 0.007 | -0.063 | 0.110 | -0.164** | -0.168** | -0.087 | -0.039 |
| Bole ratio | -0.051 | 0.024 | -0.109 | -0.055 | -0.202** | -0.188** | -0.131** | -0.097* |
| DBH | 0.315** | 0.085 | 0.259** | 0.165* | 0.085 | 0.063 | 0.228** | 0.251** |
| Fruits | 0.728** | 0.521** | 0.919** | 0.706** | 0.523** | 0.965** | 0.89** | 0.887** |
| Fruitset | 0.142 | 0.257** | 0.188* | 0.211** | 0.002 | 0.237** | 0.277** | -0.104* |
| Fruits per tree with | | | | | | | | |
| Height | -0.006 | -0.064 | 0.051 | 0.134 | 0.164** | -0.031 | 0.094* | 0.056 |
| Clear bole height | 0.009 | -0.071 | -0.087 | 0.013 | 0.051 | -0.136** | -0.034 | -0.028 |
| Bole ratio | -0.001 | -0.037 | -0.118 | -0.055 | -0.025 | -0.163** | -0.163** | -0.097* |
| DBH | 0.239** | 0.035 | 0.214** | 0.231** | 0.178* | 0.095* | 0.224** | 0.251** |
| Fruitset | 0.514** | 0.85** | 0.479** | 0.805** | 0.523** | 0.405** | 0.619** | 0.406** |

*Table 5.* – Correlation between successive years for flower (above diagonal) and fruit production (below diagonal) in two teak CSOs.

| | Topslip (CSO I) | | | | Walayar (CSO II) | | | |
|---|---|---|---|---|---|---|---|---|
| | 2003 | 2004 | 2005 | 2006 | 2003 | 2004 | 2005 | 2006 |
| 2003 | | 0.199** | 0.418** | 0.407** | | 0.684** | 0.574** | 0.575** |
| 2004 | -0.012 | | 0.295** | 0.102 | 0.111* | | 0.412** | 0.456** |
| 2005 | 0.047 | 0.132 | | 0.312** | 0.456** | 0.352** | | 0.676** |
| 2006 | 0.332** | 0.146 | 0.158* | | 0.372** | 0.314** | 0.614** | |

*Fertility variation and gene diversity*

The measures refer to the assumed gene pool of gametes formed where the clones contribute according to their registered fertility. Sibling coefficient ($\Psi$) and group coancestry were higher in CSO II than CSO I and during poor flowering years than abundant years (*Table 6*). Status number, relative status number and gene diversity were higher in CSO I compared to CSO II and in good flowering years (2005 and 2006) than poor years (2003 and 2004). In CSO II, the male fertility variation



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*Table 6.* – Fertility variation ($\Psi$), group coancestry ($\Theta$), status number (*Ns*), relative status number (*Nr*) and genetic diversity (GD) for four years in two teak CSOs.

| | 2003 | | | 2004 | | | 2005 | | | 2006 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Male | Female | Combined | Male | Female | Combined | Male | Female | Combined | Male | Female | Combined |
| Topslip (CSO I) | | | | | | | | | | | | |
| $\Psi$ | 1.73 | 2.59 | 1.97 | 2.37 | 3.48 | 2.64 | 1.70 | 1.45 | 1.49 | 1.70 | 2.51 | 2.01 |
| $\Theta$ | 0.06 | 0.09 | 0.07 | 0.08 | 0.12 | 0.09 | 0.06 | 0.05 | 0.05 | 0.06 | 0.08 | 0.07 |
| *Ns* | 8.65 | 5.78 | 7.60 | 6.32 | 4.31 | 5.68 | 8.82 | 10.37 | 10.05 | 8.82 | 5.97 | 7.48 |
| *Nr* | 0.58 | 0.39 | 0.51 | 0.42 | 0.29 | 0.38 | 0.59 | 0.69 | 0.67 | 0.59 | 0.40 | 0.50 |
| GD | 0.94 | 0.91 | 0.93 | 0.92 | 0.88 | 0.91 | 0.94 | 0.95 | 0.95 | 0.94 | 0.92 | 0.93 |
| Walayar (CSO II) | | | | | | | | | | | | |
| $\Psi$ | 5.96 | 5.38 | 4.45 | 6.80 | 5.69 | 6.22 | 2.68 | 2.45 | 2.47 | 2.50 | 2.10 | 2.26 |
| $\Theta$ | 0.15 | 0.13 | 0.11 | 0.17 | 0.14 | 0.15 | 0.07 | 0.06 | 0.06 | 0.06 | 0.05 | 0.06 |
| *Ns* | 3.36 | 3.72 | 4.50 | 2.94 | 3.52 | 3.22 | 7.46 | 8.18 | 8.11 | 7.99 | 9.53 | 8.84 |
| *Nr* | 0.17 | 0.19 | 0.22 | 0.15 | 0.18 | 0.16 | 0.37 | 0.41 | 0.41 | 0.40 | 0.48 | 0.44 |
| GD | 0.85 | 0.87 | 0.89 | 0.83 | 0.86 | 0.84 | 0.93 | 0.94 | 0.94 | 0.94 | 0.95 | 0.94 |

($\Psi_m$ = 2.5–6.79) was higher than the female fertility variation ($\Psi_f$ = 2.09–5.68) whereas in CSO I the trend was opposite ($\Psi_m$ = 1.7 to 2.37 and $\Psi_f$ = 2.51 to 3.47) except in 2005. The smallest fertility variation ($\Psi = 1.49$) was observed in CSO I in the abundant flowering year 2005 with a corresponding coancestry value of 0.05. The status number was maximum ($N_s = 10.5$) that year which is about two thirds ($N_r = 0.67$) of the census number of the orchard. Gene diversity values were consistently above 90%, the highest was 0.95 in 2005. In the abundant flowering year 2006, CSO II had the lowest fertility variation ($\Psi = 2.26$) and group coancestry (0.057). Status number ($N_s = 8.84$) was 44% of the census number for the orchard and gene diversity (0.94) was comparable to the best year of CSO I. Although CSO I generally showed low levels of fertility variation compared to CSO II, the differences between the two orchards were greatly reduced in good flowering years. CSO II in fact had lower coancestry value than CSO I in the best flowering year 2006.

## Discussion

*Flowering and fruiting in orchards*

Flower and fruit production was quite low in both the orchards to be considered for planting and breeding programmes. Even the highest yield reported for a year of about 18 kg per ha would be sufficient to raise only 5 ha of plantations assuming a 30% germination. This is less than one third of previously reported seed yield of teak seed orchards (16 ha; WELLENDORF and KAOSA-ARD, 1988). High fruit production is reported from Thailand (70 kg ha$^{-1}$) and Nigeria (244 to 734 kg ha$^{-1}$) (HEDEGART, 1976; EGENTI, 1981; MAEKAEW, 1992). Seed germination was reported to be quite low (0.97%) in CSO II and varying (5.3–16.4%) for other orchards in South India (INDIRA and BASHA, 1999; MATHEW and VASUDEVA, 2003). If the two orchards studied are considered as representative of teak CSOs in India, it is unlikely that they can meet the current planting stock requirement.

A major reason for low fruit production in orchards is lack of flowering. More than one third of trees in CSO I and 50% in CSO II remained infertile during all four years of observation seriously limiting the orchard output. Proportion of fertile trees was above 50% only once in CSO I. BILA *et al.* (1999) reported 80% of trees to be flowering in a 65-year old teak plantation in Mozambique. Fertility in 40 to 45 year old teak stands is also generally high in south India ranging from 58 to 97% (VARGHESE *et al.,* 2008). The flowering behaviour of clones originating from the same location was different in the two orchards. Four high fertility clones (KLS1–4) in CSO I were among the least fertile ones in CSO II. These clones were selected from plantations close to the location of CSO I. But two other clones (KLK1 and KLK2) that originated from a similar population showed marked difference in fertility at both locations. In CSO II, clone SBL1 originating from a location at a higher latitude than the other clones showed high level of fertility when shifted to a lower latitude (location of CSO II) similar to the trend generally observed in conifers (NIKKANEN and RUOTSALAINEN, 2000). Stand density, light intensity and site quality are the other factors that influence flowering in teak (GRAM and LARSEN, 1958; NANDA, 1962; HEDEGART, 1976).

Fruit production per tree is greatly influenced by fruitset, which generally increases when the flowering is abundant. Teak is a cross pollinated species and bees are the major pollinating agents. Pollinator limitation and their foraging behaviour, non-synchronization of flowering among clones and short duration of stigma receptivity are the major reasons for low fruit set (0.5 to 2%) in teak (NAGARAJAN *et al.,* 1996; PALUPI and OWENS, 1998). Fruitset in CSO I was lower than the expected levels (except in 2005), which resulted in low fruit production. Although the cumulative contribution of flowers by different clones was similar in the years 2003, 2005 and 2006, low fruitset in 2003 and 2006 resulted in skewed contribution of fruits by different clones (*Fig. 1*). Predation of flowers and fruits by insects has been



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reported to reduce fruitset in teak (DABRAL and AMIN, 1975).

Moderate to high heritability for flowers and fruits per tree indicate that reproductive output of trees is under genetic control. Little information is available on heritability estimates for flower and fruit production in teak. But other reproductive traits of teak like age at which first flowering occurs, flowering and fruiting phenology and dimension of floral parts are reported to be under strong genetic control (KAOSA-ARD, 1996; GUNAGA and VASEDUVA, 2002; VASEDUVA *et al.,* 2004). Seed production in teak orchards can be increased if fertility of trees is considered during ranking of clones while thinning existing orchards. On the other hand the strong genotype-environment interaction for reproductive characters indicates that it may be rather problematic to improve the reproductive output by genetic measures.

The positive correlation between tree size (diameter) and fertility traits is consistent with previously reported observations. BILA *et al.* (1999) reported a similar relationship between diameter growth and reproductive output, though high levels of variation still remained among the trees selected based on diameter. The authors attributed this variation to causes other than the overall size of the tree or the effect of suppression by neighbouring trees. The negative correlation with bole characteristics may also be a cause for the variation in fertility among trees. Clear bole height is given major emphasis during plus tree selection since it significantly influences timber volume per tree (HEDEGART *et al.,* 1975; KUMARAVELU, 1993). It is reported that in teak the first flowering occurs at the growing shoot tip resulting in forking of the main stem (GRAM and LARSEN, 1958; BOONKIRD, 1964). The early flowering trees have shorter stem boles than late flowering trees. Forking of the main stem results in a wide crown which increases the positions for development of inflorescences.

*Impact of fertility variation on orchard crop*

Although many teak CSOs are established in India and other countries, only limited information is available on fertility variation and its implications on the seed crop (KANG *et al.,* 2003; VARGHESE *et al.,* 2006). The present study shows that fertility variation is high when flowering is poor in orchards. The maximum sibling coefficient value ($\Psi$ = 6.2) was observed in CSO II during the lowest flowering year (only 16.7% of the trees flowered). This means a deviation of up to 6.2 times from random mating when all clones would have contributed equally. Plantations established from this seed source would have high coancestry and relatedness. KANG *et al.* (2003) reported fertility variation estimates for seed orchards of broadleaved species as $\Psi$ = 2.07, 3.45 and 2.62 for female, male and combined (male + female) fertility respectively. The observed $\Psi$ values for CSO I are lower or comparable to these estimates in all years except for female fertility in the lowest flowering year. In the case of CSO II, fertility variation was lower or comparable in two years but in 2003 and 2004 it was 70 to 170% higher than the expected values. However all observed values were within the range reported for broadleaved species. Fertility variation is considerably reduced ($\Psi$ = 1.49 to 2.46) when the proportion of flowering trees increased in orchards. This observation is consistent with results reported for conifer seed orchards (KJÆR, 1996; NIKKANEN and RUOTSALAINEN, 2000). Contribution of clones is more balanced in good flowering years and the differences between the two orchards were greatly reduced in such years.

Seed collection from teak orchards for progeny testing and plantation establishment should be based on the fertility variation in a given year. Progeny testing to determine breeding values of clones is generally done with seeds collected from orchards in a single year (NAGARAJAN *et al.,* 1996; SHARMA *et al.,* 1996; SWAIN *et al.,* 1999). Though seed collection for such purposes is claimed to be from good flowering years no information on fertility of clones is considered. In CSO II the number of equally contributing unrelated clones ($N_s$) was only about 9 whereas the number of flowering clones was 18 in the best flowering year, 2006. In such a situation progeny performance of clones will be greatly influenced by fertility levels of father trees. Seeds for progeny testing should preferably be collected when the fertility variation is low and the status number is more than two thirds of the census number of the orchard (KJÆR and WELLENDORF, 1998). From the results obtained in the present study it is likely that at least once in four years such abundant flowering may occur. The option of mixing seeds of a clone produced in different years may also be considered for estimating the full genetic potential of the clone. Since teak seeds can be stored for a few years without significant loss in viability such an option is practically feasible. Seed collection from orchards for plantation development may be restricted only to abundant flowering years and altogether be avoided during poor years to avoid genetic drift (KJÆR, 1996). It will also be economically unviable to organize seed collection in poor flowering years and keep the costs low. Restricting the amount of fruits collected from each clone will reduce fertility variation and increase gene diversity in the orchard progeny but further decrease the orchard output (VARGHESE *et al.,* 2006).

*Implications for establishing and managing seed production systems for teak*

Results obtained in the present study can be used to manage the existing orchards more effectively and to create new orchards. Imposing treatments like thinning, stimulation of flowering and promoting pollination are options for increasing flowering and fruiting in teak seed orchards (ALMQVIST, 2008; CHALUPKA, 2008). Variation in fertility could perhaps be compensated by intentionally adjusting the number of ramets for different clones to achieve the desired gamete frequencies, but on the other hand it is a costly measure to plant more of the least fertile clones. Removal of consistently non-flowering trees will create additional space for crown development in the fertile trees. New orchards can be established with large number of clones known to have high fertility in a similar environment. A large number of clones compensate for high fertility variation and the effective number will still be high enough. Considering the high levels of clone x site interactions, shifting of



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clones drastically from different latitudes may be avoided to prevent unbalanced representation of clones in the orchard gamete pool. Locating orchards in areas suitable for abundant flowering will also enable high orchard output and balanced gamete contribution.

While some of the options may be cost-prohibitive, most of them may not contribute to seed production in the immediate future. Further considering the inherent tendency of teak for low flowering and complex plant-pollinator interactions leading to low fruit and seed production, large number of trees is needed to produce the required amount of seeds with acceptable levels of genetic quality. Existing clonal seed orchards, typically with 15 to 30 clones may not achieve the production levels assumed at the time of planting (250 kg $ha^{-1}$; HEDEGART, 1976). Being an outcrossed species, teak harbours a major portion of diversity within the population and high intensity clonal selections do not capture it adequately (NICODEMUS *et al.,* 2005). Abundant seed production with adequate diversity is best achieved with low input breeding options like Seed Production Areas (SPA) (LINDGREN and WEI, 2007). SPAs are developed by converting plantations through rigorous thinning and account for a major share of improved seed in India. Flowering, seed production and seed germination are generally reported to be better in SPAs than seed orchards (INDIRA and BASHA, 1999; VARGHESE *et al.,* 2005). Thus they can be a source of reasonably improved seed for current planting and also for developing next generation seedling seed orchards (KJÆR *et al.,* 1999). The large number of parent trees in SPAs ensures that high level of diversity is maintained in the progeny even if the gains are modest. SPAs are timber producing areas and the seeds can be seen as a side product, while clonal seed orchards are established to get seeds only. The economy of SPA may be much better, and it is easier to defend their establishment in spite of a limited flowering.

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