

PROVENANCE VARIATION IN GROWTH, PHYSIOLOGY, ANATOMICAL CHARACTERISTICS AND FOLIAR NUTRIENT STATUS OF TEAK (*TECTONA GRANDIS*) SEEDLINGS

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JAYASANKAR, S., SUDHAKARA, K. & BABU, L. C. 2003. Provenance variation in growth, physiology, anatomical characteristics and foliar nutrient status of teak (*Tectona grandis*) seedlings. Teak seedlings representing seven provenances from Kerala (India) were examined for their differences in characteristics between June 1995 and July 1996. Seeds collected and bulked by provenance were pretreated and sown in a nursery. Data were collected on growth attributes, physiological and anatomical parameters, and foliar nutrient status of the seedlings. Large variations among provenances were observed in growth characteristics such as dry weight of stem, leaf and root, and specific leaf area. Provenances Parambikulam, Nilambur and Malayattur were found, during most of the observation intervals, to grow faster, while the local provenance (Thrissur) generally showed the lowest values. Physiological parameters such as photosynthetic rate, transpiration rate, leaf water potential and relative water content, and anatomical characteristics such as stomatal frequency were also found to be significantly higher in provenances Parambikulam, Nilambur and Malayattur. These three provenances also registered a high concentration of nutrients in different plant parts, showing their superior performance in the nursery.

Key words: Provenances - variation - *Tectona grandis* - seedlings - attributes

JAYASANKAR, S., SUDHAKARA, K. & BABU, L. C. 2003. Variasi provenans dalam ciri pertumbuhan, fisiologi, anatomi dan status nutrien daun anak benih jati (*Tectona grandis*). Kajian tentang perbezaan ciri anak benih jati yang mewakili tujuh provenans di India dijalankan antara Jun 1995 dan Julai 1996. Biji benih yang dikutip dan dikumpul mengikut provenans diprarawat dan disemai di tapak semaian. Data yang diambil ialah ciri-ciri pertumbuhan, parameter fisiologi dan anatomi, dan status nutrien daun anak benih tersebut. Perubahan yang besar antara provenans dicerap dalam ciri pertumbuhan seperti berat kering batang, daun dan akar, serta luas daun spesifik. Provenans Parambikulam, Nilambur dan Malayattur tumbuh lebih cepat pada kebanyakan selang pencerapan manakala provenans tempatan (Thrissur) paling lambat. Parameter fisiologi seperti kadar fotosintesis, kadar transpirasi, potensi air daun dan kandungan air relatif dan ciri anatomi seperti kekerapan stoma juga lebih tinggi di provenans Parambikulam, Nilambur dan Malayattur. Ketiga-tiga provenans juga menunjukkan kepekatan nutrien yang tinggi di bahagian pokok yang berbeza dan mempamerkan prestasi yang unggul di tapak semaian.

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Introduction

Physiological characteristics like water uptake and nutritional requirements are some of the important factors contributing to successful establishment and growth of tree species in provenance trials (Zech & Dreschsel 1991, Dupuy & Verhaegen 1993, Nykvist 1997). Under plantation conditions tree establishment can succeed only if the seedlings have sufficient vigour in physiological attributes and nutrient uptake level (Wild 1989, Chandrashekhara 1996).

A clear difference exists in characters among provenances of species, especially those having a wide range of natural distribution (Wright 1976). Growth, physiological characteristics and nutrient uptake capabilities are controlled by genetic factors also and vary among provenances (Kjaer & Siegismond 1996). Lebot (1996) reported that insufficient vigour in growth, physiological attributes and nutritional requirements result in the failure of some provenances when planted at certain places.

Teak (*Tectona grandis*) occupies a prime position in many plantation programmes throughout the tropical world. Teak plantation programmes in India generally use major provenances from peninsular India, including Kerala (Babu *et al.* 1997). Studies have been conducted to understand the genetic component of the variation (Dupuy & Verhaegen 1993) in teak seedlings raised from seeds of different provenances of Kerala (Kadambi 1972, Venkatesh *et al.* 1986, Bedell 1989). Another study included the variability of seed characteristics and germination parameters in the laboratory and in the nursery (Jayasankar *et al.* 1999b). Seedling characteristics in the nursery and growth behaviour of stumps prepared from one-year-old seedlings grown in polythene bags for 28 days and in the field for 6 months have also been studied (Jayasankar *et al.* 1999a). Additional observations on variations in growth, physiological attributes, anatomical characteristics and nutritional requirements of these provenances studied in the nursery are reported in this paper.

Materials and methods

Study site

The study was conducted between June 1995 and July 1996 at the nursery of the College of Forestry, Kerala Agricultural University, Vellanikkara, Kerala, India (13° 31' N, 76° 13' E; 40 m above sea-level). The site has a warm humid climate and a mean annual rainfall of 2670 mm (from 1985 to 1995) having a bimodal distribution pattern, most of which is received during the Southwest Monsoon (June to August) with its peak during June to July. A total of 355 cm of rainfall was received during the study period (June 1995–July 1996). The mean maximum temperature ranged from 28.8 °C (July) to 36.4 °C (March) and mean minimum temperature, from 21.1 °C (June) to 25.2 °C (May). The soil of the experimental site is lateritic (Oxisol) with predominant parent material of metamorphic rock of gneiss series (ustic moisture regimes and isohyperthermic temperature regimes).

Texturally it is sandy clay loam, with a bulk density of 1.37 g cm^{-3} . The chemical properties of the soil are, total N: 0.11 to 0.19% (Modified Kjeldahl method, Jackson 1958), available P: 10.5 mg kg^{-1} (Bray I method, Jackson 1958), available K: 19.8 to 25.3 mg kg^{-1} (Jackson 1958), organic C: 0.8 to 2.1% (Walkley & Black method, Jackson 1958), and pH: 6.1 to 6.8 (1:2.5 soil:solution ratio, Jackson 1958).

Experimental materials

Six middle-aged plantations (25–30 years old) of local origin were identified in each of seven teak growing regions of Kerala (Table 1). Seeds were collected from ten phenotypically superior trees in each plantation. Dominant or codominant trees with clear bole, well developed crown, bearing abundant number of seeds and devoid of infestations were selected as mother trees.

Table 1 Locality details of the *Tectona grandis* provenances

| Provenance | Latitude | Longitude | Altitude (m) | Temperature (°C) | Rainfall (mm) |
|--------------|---------------------|---------------------|--------------|------------------|---------------|
| Arienkavu | 8°44' – 9° 14' N | 76° 59' – 77° 16' E | 76–1922 | 16–33 | 2250–3080 |
| Konni | 9° 3' – 9° 85' N | 76° 4' – 77° 6' E | 60–975 | 16–29 | 2210–3640 |
| Malayattur | 10° 5' – 10° 20' N | 76° 25' – 77° E | 30–1330 | 21–33 | 2500–4500 |
| Nilambur | 11° 9' – 11° 26' N | 75° 46' – 76° 33' E | 40–2339 | 17–37 | 1400–2600 |
| Parambikulam | 10° 20' – 10° 26' N | 76° 35' – 76° 50' E | 300–1430 | 20–33 | 1180–2270 |
| Thrissur | 10° 20' – 10° 45' N | 76° 5' – 76° 45' E | 10–503 | 21–33 | 1100–3000 |
| Wynad | 11° 40' – 12° 40' N | 76° 2' – 76° 27' E | 650–1150 | 13–32 | 3800–5500 |

The floor under the selected seed mother trees was cleared of weeds, leaf litter and other undergrowth during the first and second week of January 1995 coinciding with the onset of seed fall. The seeds were collected in two to three rounds at monthly intervals. Seeds that had fallen earlier were discarded because of their immature nature. The collected seeds were spread out and dried under the sun, then stored in gunny bags at room temperature (28–31 °C).

To obtain a composite sample which is a representative of the whole provenance, sampling of seeds was carried out following a package of recommended practices (Gopal & Pattanath 1982). Equal numbers of seeds (200) collected from each lot of 60 samples (10 mother seed trees \times 6 plantations) representing a provenance were pooled to make a composite sample for a provenance. To achieve a homogeneous nature, the entire sample was spread out on a plastic sheet and mixed by scooping the seeds from side to side and from top to bottom. After thoroughly mixing, the entire seed lot was again spread out and subdivided into three equal parts to represent three replications of a provenance. This process was repeated for each provenance to obtain seven composite samples of provenances each having three subsamples (replications).

After sampling, the 600 seeds/replication were bulked, placed in numbered cloth bags and pretreated (soaking in water during the night and drying under partial shade during the day, and this cycle repeated daily for one week) prior to sowing. Three nursery beds (12 × 1.2 × 0.5 m), each representing a replication, were prepared and randomly divided into seven plots of size 1.5 × 1 m for sowing the seeds from the seven provenances, i.e. a randomized complete block design. The pretreated seeds representing replications were dibbled in appropriate plots of nursery beds at a spacing of 5 × 5 cm, so that each plot had 600 seeds in it.

Growth parameters

Destructive sampling of three seedlings per provenance from each replication was conducted at intervals of 60 days over a 360-day period. Dry weight (g plant⁻¹) of leaf, stem and root, specific leaf area (SLA) and net assimilation rate (E) (Table 2) were recorded.

Table 2 Details of growth, physiological and anatomical parameters

| Sl. No. | Parameter | Unit | Formula & description | Reference |
|---------|--------------------|---|---|--------------------------------|
| 1. | SLA | cm ² g ⁻¹ | Leaf area per plant/Leaf dry weight per plant | |
| 2. | E | g m ⁻¹ week ⁻¹ | $(W_2 - W_1 / t_2 - t_1) \times ((\text{Log}_e LA_2 - \text{Log}_e LA_1) / LA_2 - LA_1)$ where, W_2 and W_1 are the dry weight of plant at time t_2 and t_1 and LA_2 and LA_1 are the leaf area at time t_2 and t_1 | Hunt (1990) |
| 3. | A | μmol CO ₂ m ⁻² s ⁻¹ | — | |
| 4. | ψ | -MPa | — | |
| 5. | S _r | cm s ⁻¹ | — | |
| 6. | TR | mmol H ₂ O m ⁻² s ⁻¹ | — | Kozłowski <i>et al.</i> (1991) |
| 7. | RWC | % | $((FW - DT) / (TT - DT)) \times 100$ where, FW is the fresh weight of leaf punches, DT is the dry weight and TT is the turgid weight of the leaf punches after immersing in water for 12 hours | Barrs & Weatherly (1962) |
| 8. | Stomatal frequency | stomates cm ⁻² | — | Kozłowski <i>et al.</i> (1991) |

Physiological and anatomical parameters

Various physiological parameters like photosynthetic rate (A), leaf water potential (ψ), leaf diffusive resistance or stomatal resistance (S_r), transpiration rate (TR) and relative water content (RWC), and anatomical character, stomatal frequency, (Table 2) were also measured in three physiologically mature leaves

well exposed to solar radiation per seedling. In teak, a physiologically mature leaf is either the second or third leaf from the apex (Turner 1988). These observations were recorded at bimonthly intervals in three seedlings per provenance from each replication except A which was measured only at 360 days after sowing.

The photosynthetic rate (A) was measured with a portable infra-red gas analyser (IRGA - Model LI 6200, Li - Cor, USA) at 10.00 h. S_r and TR were measured with a steady state porometer (Model LI - 1600, Li - Cor, USA) at 12.00 h, and ψ with a Scholander type pressure chamber (Model 3065) at 08.00 h.

To determine RWC leaf punches were taken at 12.00 h from the leaves (three punches from each leaf) using a steel puncher having a diameter of 1.5 cm.

Stomatal frequency was recorded at 12.00 h by applying a commercial adhesive 'Quick Fix' to the central portion of the dorsal leaf lamina, allowing it to dry for 1–2 min and afterwards carefully peeling off the adhesion layer. The impression of the stomates marked on the transparent adhesive layer was carefully observed under a microscope and stomatal frequency was counted in ten microscopic fields per sample.

Foliar nutrient status

To characterise the foliar nutrient status, three seedlings per provenance from each replication were randomly selected at the end of the study (360 days after sowing, DAS). These were oven dried at 70 °C for 48 h, separated into leaf, stem and root, ground and used for the determination of N (micro-Kjeldahl method), P (vanado-molybdo phosphoric yellow colour method) and K by flame photometry (Jackson 1958).

Statistical analysis

The experimental data were statistically analysed following the analysis of variance for factorial experiment in randomised complete block (RCB) design. Significant differences were detected by 'F' tests ($\alpha = 0.05$) and Duncan's Multiple Range Test (DMRT) for comparison of means using MSTAT-C (Freed *et al.* 1988). To simplify the tables, data showing significant differences are only exhibited.

Correlation analysis

The degrees of correlation between the number of stomates and the rate of transpiration of the seedlings, between the specific leaf area and the nitrogen concentration in the leaves, and between the specific leaf area and the photosynthetic rate at 360 DAS were worked out at $p = 0.01$ level using MSTAT-C package. Inter-correlation matrix between physiological characters and the net assimilation rate at 360 DAS was calculated.

Results and discussion

Growth attributes

Partitioning of dry matter yield in seedlings of various provenances showed significant variation, especially at the later stages of observations (240–360 DAS). Leaf dry weight differed significantly among provenances only at 360 DAS (Table 3). As regards stem dry weight, Parambikulam, Nilambur and Malayattur recorded the highest values and were significantly higher than the others at 240, 300 and 360 DAS (Table 3). Root dry weight (Table 3) was also significantly superior in these provenances at 240 and 360 DAS. In all aspects Thrissur (local provenance) was the poorest performer.

Table 3 Leaf dry weight (g plant⁻¹), stem dry weight (g plant⁻¹) and root dry weight (g plant⁻¹) of seedlings of seven teak provenances, Kerala, India

| Provenance | Days after sowing | | | | | |
|--------------|---------------------|--------------------|--------------------|---------------------|--------------------|---------------------|
| | 360 | | 240 | | 360 | |
| | Leaf dry weight | | Stem dry weight | | Root dry weight | |
| Arienkavu | 11.91 ^{bc} | 4.67 ^{bc} | 8.15 ^{bc} | 13.75 ^c | 6.77 ^{bc} | 20.46 ^c |
| Konni | 11.43 ^{bc} | 3.97 ^{cd} | 9.75 ^{bc} | 16.04 ^{bc} | 5.36 ^c | 24.00 ^{bc} |
| Malayattur | 16.40 ^a | 7.17 ^a | 14.29 ^a | 25.44 ^a | 8.61 ^a | 29.07 ^a |
| Nilambur | 16.71 ^a | 8.81 ^a | 14.87 ^a | 25.94 ^a | 9.89 ^a | 30.23 ^a |
| Parambikulam | 17.24 ^a | 8.08 ^a | 14.96 ^a | 26.14 ^a | 9.13 ^a | 30.97 ^a |
| Thrissur | 9.83 ^{cd} | 4.94 ^{bc} | 6.39 ^{cd} | 10.06 ^d | 6.19 ^{bc} | 18.20 ^c |
| Wynad | 11.81 ^{bc} | 4.21 ^{bc} | 8.42 ^{bc} | 13.92 ^c | 5.99 ^{bc} | 21.53 ^c |
| CD (0.05) | 4.31 | 1.31 | 4.49 | 3.51 | 1.42 | 4.70 |
| SEM (±) | 1.55 | 0.47 | 1.62 | 1.43 | 0.51 | 1.70 |

Within a column values with the same alphabets (superscripts) do not differ significantly at any given time.

The provenances which exhibited better performance during the initial stage of growth were found to be better throughout the growth observation period. Similar results have been obtained by Rai *et al.* (1982), Gupta *et al.* (1992) and Chadhar (1994). Glover (1987) suggested that root growth patterns generally follow the same trend of height growth patterns. An examination of the seedling height, root length and collar diameter of seedlings in the nursery and shoot height and collar girth of stumps after six months of planting revealed that Parambikulam, Nilambur and Malayattur provenances had higher means and were statistically superior to other provenances tested (Jayasankar *et al.* 1999a). Thrissur provenance recorded the lowest mean in this respect.

Significant variation was observed with respect to specific leaf area (Table 4) during the final stages (240 DAS onwards) only. Nilambur, Malayattur and Parambikulam registered the largest specific leaf area and were significantly higher than the others tested. The local provenance (Thrissur) had the lowest specific leaf area during most of the growing stages. It may be presumed that the available

solar energy was more effectively intercepted by Nilambur, Malayattur and Parambikulam due to higher leaf biomass implying greater potential for photosynthetic carbon fixation (Kozłowski *et al.* 1991).

Table 4 Specific leaf area ($\text{cm}^2 \text{g}^{-1}$), net assimilation rate ($\text{g cm}^{-2} \text{week}^{-1} \times 10^{-1}$) and leaf water potential ($-\text{MPa}$) of seedlings of seven teak provenances, Kerala, India

| Provenance | Days after sowing | | | | | | | | | |
|---------------|---------------------|----------------------|----------------------|-----------------------|--------------------|----------------------|--------------------|-------------------|-----|-----|
| | 240 | | | 300 | | 360 | | 240 | 180 | 240 |
| | Specific leaf area | | | Net assimilation rate | | Leaf water potential | | | | |
| Arienkavu | 172.44 ^b | 227.74 ^{bc} | 221.21 ^c | -4.29 ^b | 6.34 ^{bc} | 0.80 ^c | 1.57 ^{bc} | 0.78 ^c | | |
| Konni | 168.55 ^b | 245.70 ^b | 221.75 ^c | -4.44 ^b | 6.22 ^{bc} | 0.78 ^c | 1.57 ^{bc} | 0.74 ^d | | |
| Malayattur | 186.57 ^a | 288.03 ^a | 273.39 ^{ab} | 0.40 ^a | 8.94 ^a | 0.89 ^{ab} | 1.73 ^a | 0.87 ^a | | |
| Nilambur | 181.83 ^a | 291.96 ^a | 280.91 ^a | 1.08 ^a | 8.65 ^a | 0.90 ^{ab} | 1.72 ^a | 0.92 ^a | | |
| Parambikulam | 186.55 ^a | 287.62 ^a | 270.71 ^{ab} | 0.89 ^a | 8.68 ^a | 0.93 ^a | 1.75 ^a | 0.89 ^a | | |
| Thrissur | 159.41 ^c | 206.55 ^c | 204.25 ^{cd} | -4.12 ^b | 6.22 ^{bc} | 0.78 ^c | 1.45 ^c | 0.70 ^c | | |
| Wynad | 126.33 ^d | 243.85 ^b | 193.74 ^{cd} | 3.12 ^{ab} | 4.89 ^c | 0.86 ^{bc} | 1.59 ^{bc} | 0.83 ^b | | |
| CD (0.05) | 6.23 | 34.32 | 31.82 | 3.87 | 2.29 | 0.11 | 0.12 | 0.03 | | |
| SEM (\pm) | 2.19 | 12.07 | 11.83 | 1.36 | 0.81 | 0.04 | 0.04 | 0.01 | | |

Within a column values with the same alphabets (superscripts) do not differ significantly at any given time.

The mean values of net assimilation rate (E) were significantly different at 240 and 360 DAS (Table 4). Nilambur, Malayattur and Parambikulam were significantly higher than the others, while Konni and Wynad recorded the lowest values during these stages. Generally, E is an index of the productive efficiency of the plants calculated not in relation to the total dry weight (like relative growth rate), but in relation to the total leaf area and it is an index of leaf efficiency (Hunt 1990). Increasing E points to an increase in efficiency of the available leaf area (Kallarackal & Somen 1992). Plants with higher E are able to maintain better water balance during the periods of limited water availability and thus are able to maintain greater net photosynthetic rates during these periods (Kolb *et al.* 1991). The E of seedlings of the provenances decreased considerably due to shedding of leaves during dry summer months (180 to 240 DAS) and increased again after this. However, seedlings from Nilambur, Parambikulam and Malayattur exhibited a smaller decrease because of the reduced amount of leaf shedding compared to Konni, Arienkavu, Thrissur and Wynad. Jayasankar *et al.* (1999a) have also observed similar results with respect to relative growth rate (RGR) (data not presented here). This shows that the negative effect of leaf shedding and water stress on RGR and E was negligible in Nilambur, Parambikulam and Malayattur provenances.

Physiological and anatomical parameters

Photosynthetic rates (A) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of the provenances (assessed only at 360 DAS, data not given as table) were significantly different at 360 DAS ($\text{CD}(0.05) = 0.0177$, $\text{SEM}(\pm) = 0.0058$). Parambikulam recorded the highest A ($4.59 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) followed by Nilambur (4.55) and Malayattur (4.53): these were significantly superior to the others tested. The local provenance (Thrissur) recorded the lowest value (4.23), while Konni (4.44), Arienkavu (4.42) and Wynad (4.38) were not significantly different. A higher photosynthetic rate implies greater efficiency of the plants to grow and utilize maximum light at optimum light intensities (Naidu *et al.* 1998). Natarajan *et al.* (1989) reported that photosynthetic rate may be used as a criterion for the screening of provenances and selecting superior ones for plantation programmes.

The physiological parameters showed significant variations between provenances at different periods. Leaf water potential (ψ) showed significant variation only at 120, 180 and 240 DAS (Table 4). Parambikulam, Nilambur and Malayattur showed higher values during these periods and were significantly superior to the others tested. This may be attributed to high resistance of xylem vessels in controlling the water status in plants as reported by Abbssenac and Nour (1986) in cedars and pines. High values of ψ especially at moisture deficient conditions indicate the efficiency in maintaining the water status by optimum absorption. Leaf water potential is considered as a direct indicator of water status of the plants. Moderate decrease in water status of the soil is accompanied by a steep decrease in the leaf water potential (Cavelier 1990).

The highest leaf diffusive resistance (S_r) was associated with the local provenance (Thrissur) during most of the stages, while Malayattur, Nilambur and Parambikulam showed lower S_r values throughout the experimental period (Table 5). In general, S_r increased with the decreasing water status of the soil. The rise in S_r was steeper at the beginning of the summer season (180 DAS) but showed a significant drop at peak dry period. This may be due to the decrease in the number of leaves and continued transpiration by the remaining few leaves (Cermak 1989, Cui & Smith 1991). Consequently, the S_r was in inverse proportion to the level of transpiration rate.

The highest rate of transpiration (TR) was noted in Malayattur provenance at all stages followed by Nilambur and Parambikulam provenances (Table 5). This was significantly higher compared to the others throughout the trial period. The lowest TR rate was recorded by Thrissur.

Table 5 Leaf diffusive resistance ($\text{cm}^{-2}\text{s}^{-1}$) and transpiration rate ($\text{m mol H}_2\text{O m}^{-2}\text{s}^{-1}\text{plant}^{-1}$) of seedlings of seven teak provenances, Kerala, India

| Leaf diffusive resistance | | | | | | |
|---------------------------|--------------------|---------------------|---------------------|---------------------|---------------------|--------------------|
| Provenance | Days after sowing | | | | | |
| | 60 | 120 | 180 | 240 | 300 | 360 |
| Arienkavu | 9.04 ^a | 12.68 ^{ab} | 14.23 ^{ab} | 2.44 ^{ab} | 2.64 ^{bc} | 7.66 ^b |
| Konni | 7.55 ^b | 12.40 ^{ab} | 12.19 ^b | 2.41 ^{ab} | 2.43 ^{bc} | 5.45 ^{cd} |
| Malayattur | 4.23 ^d | 6.10 ^d | 7.40 ^c | 2.10 ^c | 2.29 ^c | 4.26 ^d |
| Nilambur | 4.39 ^d | 6.47 ^d | 8.57 ^c | 2.27 ^{bc} | 2.30 ^c | 4.28 ^d |
| Thrissur | 9.29 ^a | 13.57 ^a | 16.00 ^a | 2.66 ^a | 3.39 ^a | 9.29 ^a |
| Parambikulam | 4.73 ^d | 7.70 ^c | 8.96 ^c | 2.37 ^b | 2.39 ^c | 4.40 ^d |
| Wynad | 5.45 ^{cd} | 9.01 ^c | 15.72 ^a | 2.51 ^{ab} | 2.71 ^{bc} | 9.20 ^a |
| CD (0.05) | 1.38 | 1.98 | 2.27 | 0.20 | 0.27 | 1.36 |
| SEM (\pm) | 0.50 | 0.71 | 0.82 | 0.17 | 0.10 | 0.49 |
| Transpiration rate | | | | | | |
| Arienkavu | 3.55 ^c | 2.62 ^c | 2.38 ^b | 18.38 ^{ab} | 16.30 ^b | 4.89 ^c |
| Konni | 4.47 ^{bc} | 2.62 ^c | 2.05 ^b | 18.60 ^{ab} | 15.17 ^{bc} | 5.55 ^{bc} |
| Malayattur | 6.97 ^a | 5.36 ^a | 4.67 ^a | 19.93 ^a | 17.96 ^a | 7.02 ^a |
| Nilambur | 6.91 ^a | 5.37 ^a | 4.11 ^a | 19.90 ^a | 17.94 ^a | 6.98 ^a |
| Thrissur | 3.55 ^c | 2.34 ^c | 1.97 ^c | 16.08 ^b | 10.39 ^c | 3.20 ^d |
| Parambikulam | 6.68 ^a | 4.52 ^{ab} | 3.78 ^a | 19.08 ^a | 17.87 ^a | 6.92 ^a |
| Wynad | 5.55 ^b | 3.56 ^b | 1.97 ^c | 16.09 ^b | 16.07 ^b | 3.92 ^d |
| CD (0.05) | 1.04 | 0.85 | 0.60 | 1.92 | 1.74 | 1.03 |
| SEM (\pm) | 0.38 | 0.31 | 0.22 | 0.69 | 0.63 | 0.37 |

Within a column values with the same alphabets (superscripts) do not differ significantly at any given time.

The highest relative water contents (RWC) were recorded for Nilambur, Parambikulam and Malayattur (Table 6). These were significantly greater than most of the others throughout the study period. Thrissur had the lowest RWC. A moderate decrease in the RWC during summer months indicates that teak may be moderately tolerant to water stress. However, significant differences in RWC among the provenances indicate that Nilambur, Parambikulam and Malayattur are more efficient in maintaining the water status by optimum absorption compared with other provenances (Kozłowski 1982, Kolb *et al.* 1991).

Stomatal frequency of seedlings was significantly different among provenances throughout the experimental period (Table 6). Parambikulam, Nilambur and Malayttur had significantly higher values than the others throughout the study period while the minimum values were given in the local provenance at the early stages (60 - 180 DAS) and in Wynad from 240 DAS onwards. A positive correlation between the number of stomates and the rate of transpiration was observed ($r = 0.847$) confirming the results of Vandermozel *et al.* (1989) in *Eucalyptus* species and Rajesh *et al.* (1997) in four species including teak.

Table 6 Relative water content (%) and stomatal frequency (stomates cm⁻²) of seven teak provenances, Kerala, India

| Provenance | Days after sowing | | | | | |
|--------------------|--------------------|-------------------|--------------------|--------------------|--------------------|--------------------|
| | 60 | 120 | 180 | 240 | 300 | 360 |
| Arienkavu | 36.9 ^{bc} | 45.4 ^b | 32.8 ^{bc} | 30.6 ^{bc} | 32.0 ^b | 37.2 ^b |
| Konni | 34.7 ^c | 46.3 ^b | 27.8 ^c | 26.6 ^c | 32.0 ^b | 36.4 ^b |
| Malayattur | 50.2 ^{ab} | 51.8 ^a | 43.1 ^{ab} | 42.7 ^a | 43.7 ^{ab} | 49.6 ^{ab} |
| Nilambur | 50.8 ^{ab} | 53.0 ^a | 48.1 ^a | 44.1 ^a | 48.5 ^a | 53.7 ^a |
| Parambikulam | 54.6 ^a | 52.9 ^a | 44.7 ^a | 41.7 ^{ab} | 45.2 ^{ab} | 50.4 ^a |
| Thrissur | 36.9 ^c | 42.4 ^b | 26.4 ^c | 25.3 ^c | 33.3 ^b | 36.2 ^b |
| Wynad | 40.0 ^{bc} | 45.7 ^b | 32.4 ^{bc} | 30.7 ^c | 34.0 ^b | 36.3 ^b |
| CD (0.05) | 12.57 | 4.57 | 10.54 | 10.61 | 12.38 | 12.30 |
| SEM (±) | 4.42 | 1.61 | 3.71 | 3.73 | 4.35 | 4.32 |
| Stomatal frequency | | | | | | |
| Arienkavu | 2110 ^d | 2660 ^c | 4190 ^c | 4130 ^d | 4060 ^d | 4440 ^c |
| Konni | 2110 ^d | 2990 ^c | 4290 ^d | 4020 ^c | 4100 ^c | 4340 ^d |
| Malayattur | 2360 ^b | 3520 ^a | 5290 ^a | 4230 ^c | 4560 ^b | 4930 ^b |
| Nilambur | 2380 ^a | 3320 ^b | 4790 ^b | 4720 ^a | 4540 ^b | 4920 ^b |
| Parambikulam | 2380 ^a | 3190 ^c | 4710 ^c | 4670 ^b | 4680 ^a | 4980 ^a |
| Thrissur | 1880 ^c | 2880 ^f | 4040 ^f | 4140 ^d | 3960 ^c | 4290 ^c |
| Wynad | 2330 ^c | 3080 ^d | 4010 ^g | 4020 ^c | 3600 ^f | 4210 ^f |
| CD (0.05) | 12.09 | 27.30 | 28.82 | 28.38 | 22.87 | 26.45 |
| SEM (±) | 4.25 | 9.60 | 10.13 | 9.98 | 8.04 | 9.30 |

Within a column values with the same alphabets (superscripts) do not differ significantly at any given time.

Coefficients of correlation between the physiological parameters and E at 360 DAS (Table 7) revealed maximum correlation between A and TR (0.932) and minimum between S_r and TR (-0.985), confirming the results of Naidu *et al.* (1998) in tropical deciduous tree species.

Table 7 Inter-correlation matrix between the physiological characters and the net assimilation rate at 360 DAS in seven teak provenances, Kerala, India
(A - Photosynthetic rate, S_r - Leaf diffusive resistance, TR - Transpiration rate, ψ - Leaf water potential, RWC - Relative water content, and E - Net assimilation rate)

| Character | A | S_r | TR | ψ | RWC |
|-----------|----------|----------|---------|---------|---------|
| S_r | -0.892** | | | | |
| TR | 0.932** | -0.985** | | | |
| ψ | 0.824** | -0.784** | 0.826** | | |
| RWC | 0.813** | -0.823** | 0.869** | 0.924** | |
| E | 0.528* | -0.663** | 0.682** | 0.685** | 0.718** |

** Significant at 0.01 % level;

* Significant at 0.05 % level.

Foliar nutrient concentration

Concentrations of N, P and K in different plant parts showed highly significant variations among the provenances except for N concentration in the stem (Table 8). Concentrations of N, P and K in the leaves were largest in Malayattur, while the lowest N concentration was recorded by the local provenance (Thrissur). Arienkavu recorded the lowest P and K concentrations. P and K concentrations in the stem were highest in Parambikulam and Malayattur, the lowest P concentration was in the local provenance and lowest K concentration was in Wynad. N concentration in the roots was highest in Nilambur provenance and was significantly superior to the others; the lowest concentration was in the local provenance. Wynad exhibited the maximum concentration of P in the roots, while K concentration was higher in Parambikulam. Arienkavu was characterized by the lowest concentration of P and K in the roots.

Table 8 Concentration of nutrients (%) in different plant parts of seedlings of seven teak provenances

| Provenance | Leaf | | | Stem | | | Root | | |
|---------------|--------------------|--------------------|-------------------|------|---------------------|--------------------|--------------------|--------------------|--------------------|
| | N | P | K | N | P | K | N | P | K |
| Arienkavu | 1.54 ^{bc} | 0.09 ^{bc} | 0.32 ^c | 0.50 | 0.03 ^{bc} | 0.25 ^b | 0.55 ^d | 0.03 ^b | 0.09 ^c |
| Konni | 1.56 ^{bc} | 0.08 ^c | 0.33 ^c | 0.55 | 0.03 ^{bc} | 0.24 ^{bc} | 0.66 ^{cd} | 0.05 ^{ab} | 0.10 ^c |
| Malayattur | 2.62 ^a | 0.12 ^a | 0.60 ^a | 0.66 | 0.04 ^{abc} | 0.33 ^a | 0.81 ^{bc} | 0.04 ^{ab} | 0.16 ^b |
| Nilambur | 1.97 ^b | 0.11 ^{ab} | 0.45 ^b | 0.66 | 0.04 ^{ab} | 0.29 ^{ab} | 1.11 ^a | 0.04 ^{ab} | 0.16 ^b |
| Parambikulam | 1.92 ^b | 0.11 ^{ab} | 0.56 ^a | 0.61 | 0.05 ^a | 0.29 ^{ab} | 0.91 ^b | 0.03 ^b | 0.20 ^a |
| Trichur | 1.46 ^c | 0.09 ^{bc} | 0.36 ^c | 0.56 | 0.03 ^c | 0.23 ^{bc} | 0.50 ^d | 0.03 ^b | 0.12 ^{bc} |
| Wynad | 1.56 ^{bc} | 0.09 ^{bc} | 0.38 ^c | 0.55 | 0.03 ^{bc} | 0.18 ^c | 0.61 ^d | 0.06 ^a | 0.10 ^c |
| CD (0.05) | 0.39 | 0.26 | 0.07 | ns | 0.01 | 0.07 | 0.19 | 0.02 | 0.04 |
| SEM (\pm) | 0.14 | 0.01 | 0.02 | 0.06 | 0.01 | 0.02 | 0.07 | 0.01 | 0.01 |

Within a column values with the same alphabets (superscripts) do not differ significantly at any given time.

ns: not significant.

Adams and Attiwill (1984) suggested that a relative abundance of N in the plant vegetative parts shows the efficiency of utilizing N. Atkinson (1983) reported that the chances of having nutrient deposition in the plant parts especially leaves are likely to be higher in tree species including teak which absorb and utilise the nutrients effectively from the soil. The nutrients that remain after sufficient utilisation by the plants are probably deposited in the plant parts when the absorption rate is higher.

Jurik (1986) found a strong positive correlation between leaf mass per plant and net photosynthesis for a variety of hardwood species. His experiment specifies that greater specific leaf area may indicate the supply of more leaf N to the photosynthetic machinery for assimilation. The leaves with a high nitrogen content can utilize light of high photon flux densities (PFDs) more efficiently for photosynthesis than those with low nitrogen content (Mooney & Gulmon 1979).

Our study also observed a positive correlation between SLA and N concentration in the leaves ($r = 0.874$) and between SLA and A ($r = 0.931$). Hence it is not surprising that Parambikulam, Nilambur and Malayattur, which exhibited the maximum amount of leaf dry weight and specific leaf area, were characterized by higher leaf N concentration, higher photosynthetic rate and higher growth potential.

The nutrient concentration in the leaves and internal nutrient cycling in a variety of species largely depend on the inherent properties of the species and provenances rather than the quantity of nutrients in the soil in which they grow (Gagnon 1964, Datta 1996). Lee (1988) pointed out that the lowest concentration of nutrients occurs in slow-growing provenances of teak which may be less nutrient-demanding provenances. Studies are going on to determine the nutrient status of the soils of the plantations from which the seeds were procured and to correlate to the leaf nutrient status of trees growing in these plantations and seedling nutrient status of the provenances planted in the experimental field.

Conclusions

Seedling characteristics of seven provenances of teak (*Tectona grandis*) from Kerala (India) studied in the nursery revealed that provenance variations significantly influenced the growth attributes, physiological and anatomical characteristics, and nutrient uptake. Parambikulam, Nilambur and Malayattur provenances had greater values for most of the parameters tested throughout the experimental period. The local provenance (Thrissur) consistently recorded the lowest values. The present set of studies, which include seeds (Jayasankar *et al.* 1999b), seedlings in the nursery and growth of stumps in the main field (Jayasankar *et al.* 1999a), have conclusively proved that Parambikulam, Nilambur and Malayattur provenances perform better than other provenances. Further studies at plantation level are required to confirm these findings.

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