Environmental implications of Gondwana wood studies in India

A RAJANIKANTH AND RAJNI TEWARI

Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226 007, India. E-mail: arajanikanth@hotmail.com and rajnit@flashmail.com

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ABSTRACT


A synthesis of fossil gymnospermous woods from various Gondwana basins of India is presented, and characters of growth rings in the secondary wood, particularly tracheidal cell characters, are evaluated for possible palaeoclimatic signals. Permian fossil woods are mostly recorded from the Damuda, Wardha and Pranhita-Godavari basins. Growth rings are common in many of these species and suggest strong seasonality. Triassic woods are poorly known from the South Rewa Gondwana Basin; the paucity of growth rings suggests a lack of marked seasons. Available evidence on Jurassic woods from the Pranhita-Godavari Graben indicates lack of consistency in the growth ring distribution. Early Cretaceous fossil woods recorded from the Damuda, Pranhita-Godavari, East-Coast and Kutch basins mostly show growth rings, which suggest prevalence of distinct seasons. Ecological factors coupled with phenotypic plasticity, i.e., variation with the same genotype as a function of environmental differences (genetic flexibility) probably dictated wood accumulation patterns in Indian Gondwana woods. However, palaeo-latitudeinal and palaeo-physiographic constraints influenced habitats, and subsequent taphonomic processes resulted in incomplete understanding of palaeoclimate. In the absence of contemporary meteorological data during Gondwana times on what is now on the Indian continent, fossil woods constitute an important tool for understanding the past impact of climate on tree growth.

Key-words—Wood, Gondwana, Palaeoclimate, Growth rings, Seasons.

भारत में गोंडवाना कांड अध्ययन की पर्यावरणीय गुणवत्ता अन्तर्गतिक
अन्य माना कांड एवं रास्ती विभाजन

सारांश

भारत के प्राचीन गोंडवाना ध्रुवियों के प्राचीन अन्वयकीय कांड जीवाश्म के अभिलेखों का संकलन प्रदर्शित किया गया है तथा विशेषकर कांड में वृद्धि वल्लय के लक्षण (विशेषकर वाहिनीविद कोशिका लक्षण) स्वभावी पुरुषजातवादिक संरक्षण हेतु नूतन किया गया है। प्राचीन कांड जीवाश्म अध्ययन दायुदा, वर्त्तमान प्रारंभिक-गोंडवाना ध्रुवियों से अभिलेखित किए गए हैं। इन वृद्धि कई प्रजातियों में सामान्यता वृद्धि वल्य होती है तथा मजबूत अनुमित होने का सुझाव दिया है। विभिन्न राशि गोंडवाना में अधिक इतिहासकारों की अवधारणाओं को आधारण है। वृद्धि वल्यों की कठिन अस्तुति भूमि विभेद का संकेत दिखाती है। प्रारंभिक-गोंडवाना ध्रुवियों के प्राचीन जुगरूकक कांडों पर उपलब्ध प्रमाण वृद्धि वल्य विश्लेषण एक संदेशों की कथा का संकेत है। दायुदा, प्रारंभिक-गोंडवाना, पूर्व-पूर्वी एवं कांड ध्रुवियों से अभिलेखित प्रारंभिक विभिन्न कांड जीवाश्म अध्ययन वृद्धि वल्य प्रदर्शित करते हैं जो कि बुध कीमतों का बायकाला घटी है। भारतीय
INTRODUCTION

THE Gondwana Sequence, confined to the Southern Hemisphere, ranges from the Early Palaeozoic to the Early Cretaceous. In India, the sediments referred to the Gondwana are invariably fluvo-lacustrine deposits with occasional paralic intercalations. The definition, geographic extent and age of the Indian Gondwana have been subjects of speculation, and various views have been expressed that re-evaluate and reassess the concept (Oldham, 1893; Fox, 1931; Chakravarty, 1974; Dutta et al., 1983; Venkatachala & Maheshwari, 1988, 1991a; Venkatachala et al., 1993; Tiwari, 1999; Rajanikanth et al., 2000). Both lithologic and biologic evidences have been utilised to divide the Indian Gondwana into Lower, Middle and Upper units. This standard succession has also been floristically demarcated into the Glossopteris, Dicroidium and Ptilophyllum floras, corresponding to Permian, Triassic and Jurassic-Early Cretaceous ages (Bose, 1966; Lele, 1964; Shah et al., 1971; Saksena, 1974). The growth of luxuriant vegetation during Indian Gondwana sedimentation is evident from terrestrial plant fossil remains in the form of leaves, woods, seeds, fructifications, spores and pollen, roots and associated fragments. These are variously preserved as impressions, compressions and petrifications (Seward & Sahni, 1920; Sahni, 1928, 1931; Lakhanpal et al., 1976; Shah, 1977; Bose et al., 1990; Venkatachala & Maheshwari, 1991; Chandra & Tewari, 1991; Rajanikanth & Prakash, 1994; Sengupta, 1998; Shah & Bandypadhyay, 1998). Petrified fossil woods showing growth rings have been recorded from different Indian Gondwana basins – Damuda, Rajmahal, South Rewa, Kutch, Son-Mahanadi, Satpura, Pranhita-Godavari and associated east-coast basins (Fig. 1).

Plant evolution has involved appearance of numerous ecological strategies. Climatic regimes have influenced plant growth and development through geological ages. Study of anatomical details in fossil woods is a reliable tool for inferring environmental preferences and differentiation of seasons. Gondwana basins of India are well known for gymnosperm wood fossils, most of which occur as detached fossil axes/stems. These are assigned to various 'form' taxa.

Gymnosperms, a large and ancient assemblage of lines including pteridosperms, cycadophytes and coniferophytes, were the most important land plants for about 150 million years, until they were outnumbered by the flowering plants in the mid Cretaceous; their remnants have survived in more restricted niches from 100 million years ago to the present. The present-day occurrence of members of Araucariaceae, Podocarpaceae, Taxaceae and Cupressaceae in the Southern Hemisphere is well known (Rao, 1963; Ramanujam, 1968). The latter two families are primarily, confined to the Northern Hemisphere (Florin, 1940; Krassilov, 1978).

APPROACH

Plant growth is generally timed to coincide with favourable environmental conditions. Growth patterns preserved in the tissues through geological ages reflect changing climatic conditions (Chaloner & Creber, 1990). Tree growth is an adaptive strategy to exploit and dominate the habitat above ground. The wood portion of trees integrates signatures of past climatic changes, since availability of sunlight, water and related ecological factors dictate growth of wood tissues. Xylem tissue is a tough and hard substance that conducts water and inorganic salts throughout the plant.
and further provides it with mechanical strength. Woods derived from the various plant parts, such as stumps, trunks and branches, possess individual distinct characters (Bijlsman & Lorschehehe, 1997), which in turn can be used to analyse environmental influences. It is well known that seasonal changes in water, temperature and light conditions cause periodic changes in the size of tracheids or vessels. The thickness and regularity of wood accumulation are positive parameters that can be used to infer seasonal variations (Hiroyuki et al., 1995). Independent palaeobotanical approaches to such qualitative attributes of fossil woods as tree ring data are useful for understanding effects of climatic change through time (Hughes et al., 1982). The prevalence of uniform growth conditions, inter-annual consistency and causes of seasonal dormancy can also be interpreted through studies of wood anatomy (Creber, 1977).

Plants are spatially fixed and must be adapted to atmospheric and substrate conditions. They are therefore tightly constrained by the climatic regime under which they grow (Knoll, 1986; Falcon Long, 2000). Analysis of past climates can be conducted through two approaches - extrapolation of climatic tolerances of living taxa backward in time, and use of taxon-independent structural adaptations or responses of plants to environment.

Physiological adaptations are reflected in morphology, anatomy and chemistry. These are solutions to environmental stresses placed upon terrestrial organisms that evolved early in plants, in relation to temperature, water availability, nutrient supply, gas exchange and light capture. These solutions are largely required evolution of some basic structures such as tracheids, stomata, roots, etc. that evolved at particular points in the phylogeny of land plants and are taxon-independent (Chapman, 1994).

The palaeobotanical record reveals solutions to environmental problems at a variety of spatial and temporal scales (Knoll & Niklas, 1987). Growth rings are often used as indicators of palaeolatitude. The approach to the study of fossil woods includes long-term data storage and deciphering of climate over decades to centuries based upon growth rings (Fritz Hans, 1988).

Seasonal variations influence wood accumulation patterns, and growth ring studies thus provide clues to prevailing environmental conditions. The modulated activity of the cambium produces growth rings. Parameters such as ring width, early–late wood ratio, and other anatomical and chemical features are directly influenced by ambient environmental conditions during the growing period. The scientific discipline concerned with dating and interpreting past events, particularly palaeoclimates and climatic trends, based on the analysis of tree rings is referred as Tree Ring Dating or Dendrochronology (Fritts, 1976). Similar studies, emphasising estimates of climate at a particular time more than dating, have been also widely used for pre-Quaternary periods (Creber, 1977; Jefferson, 1982; Creber & Chaloner, 1984a, b, 1985; Chaloner & Creber, 1990; Francis, 1986; Parrish & Spicer, 1988; Yadav, 1991; Yadav & Bhattacharyya, 1994; Brison Philippe & Thevenard, 2001).

LIMITATIONS

The potential for identifying the fossil wood specimens with living taxa greatly diminishes with geological age. There are many limitations in applying wood structure studies to pre-Quaternary climatic interpretations: florae are more remote in age; ecological requirements of past plants could have differed from those of their closest living relatives; most of the taxa are of unknown affinity and association with parent plants; physiological analogy with modern plants may be speculative; the selective process of fossilisation restricts definite palaeoclimatic inferences and only generalisations can be drawn (Creber & Chaloner, 1985; Dorf, 1963; Crawley & North, 1991; Boulter et al., 1988; Cranquist, 1978) For example, the potential of preservation was highest for perennial plants that had an upright woody main stem and were tallest at maturity. Besides, most of the wood taxa are artificial and a nomenclatural uniformity on global scale is necessary for any meaningful inferences (Bamford & Philippe, 2001; Philippe et al., 2004). With these limitations, the present synthesis on Indian Gondwana woods is attempted, focusing on secondary woods of naked-seeded plants that potentially possess growth rings, their geographic distribution and tracheidal cell characteristics (Fig. 2). Variability in tracheidal cell size, shape, thickness and other parameters is assessed to deduce climatic changes. Overall there are about 35 artificial genera and 106 species known from the different Indian Gondwana basins ranging from Permian; to Triassic, Jurassic and Early Cretaceous ages.

INDIAN GONDWANA WOODS

Permian

The Permian woods show pycnoxylic xylem with prominent growth rings often with resin ducts and are known from the Damuda, Wardha and Pranhita-Godavari basins, assignable to the Barakar, Raniganj and Kamthi horizons. These woods have been classified into 28 form genera assignable to 68 species (Fig. 2).

The number of genera and species reported increases from the bottom to the top of the Permian Sequence: from six genera and nine species in the Barakar Horizon, to 12 genera and 22 species in the Raniganj. Early Permian Indian wood records (Barakar Formation) are scarce. Ecological inferences drawn about the Early Permian times on the basis of other plant evidences suggest prevalence of cold temperate
### PERMIAN

<table>
<thead>
<tr>
<th>TAXA *</th>
<th>AUTHORS</th>
<th>HORIZON</th>
<th>EARLY WOOD</th>
<th>LATE WOOD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agathoxylon vestitanense</td>
<td>Agashe &amp; Prasad 1989</td>
<td>Kamthi</td>
<td>120-130 tracheids deep, 45-66 μm</td>
<td>3-5 tracheids deep, 20-30 μm</td>
</tr>
<tr>
<td>A. zaranense</td>
<td>Agashe &amp; Prasad 1989</td>
<td>Kamthi</td>
<td>110-120 tracheids deep, 65 μm</td>
<td>3-6 tracheids deep, 40-50 μm</td>
</tr>
<tr>
<td>A. cataractaensis</td>
<td>Maheshwari 1972</td>
<td>Barakar</td>
<td>1.5-6.5 mm deep, 25-45 x 25-44 μm</td>
<td>5-7 tracheids deep, 14-25 μm, walls 7 μm</td>
</tr>
<tr>
<td>A. bhivkhilense</td>
<td>Agashe &amp; Prasad 1989</td>
<td>Kamthi</td>
<td>120-130 tracheids deep, 60 x 30 μm</td>
<td>2-4 tracheids deep, 30 x 2 μm</td>
</tr>
<tr>
<td>A. bradshawianum</td>
<td>Bajpai &amp; Maheshwari 1986</td>
<td>Raniganj</td>
<td>60-75 tracheids deep, 26-52 x 32.5-52 μm, walls 13-19 μm</td>
<td>4-5 tracheids deep, 13-19.5 x 26-52 μm, walls 13-19.5 μm</td>
</tr>
<tr>
<td>A. gondwanaense</td>
<td>Maheshwari 1972</td>
<td>Barakar</td>
<td>40-50 tracheids deep, 35-70 μm</td>
<td>17-28 μm, wall 9-28 μm</td>
</tr>
<tr>
<td>A. kharkhariense</td>
<td>Maheshwari 1972</td>
<td>Barakar</td>
<td>40-70 tracheids deep, 42-56 μm</td>
<td>2-3 tracheids deep, walls 15-28 μm</td>
</tr>
<tr>
<td>A. kothariensis</td>
<td>Agashe &amp; Prasad 1983</td>
<td>Kamthi</td>
<td>70-80 tracheids deep, 50 x 40 μm</td>
<td>30 x 20 μm</td>
</tr>
<tr>
<td>A. kumarpurensis</td>
<td>Agashe et al., 1981</td>
<td>Kamthi</td>
<td>44-79 x 31-63 μm, walls 9-24 μm</td>
<td>11-32 x 31-48 μm, walls 7-17 μm</td>
</tr>
<tr>
<td>A. latiense</td>
<td>Agashe &amp; Gowda 1978</td>
<td>Kamthi</td>
<td>150-160 tracheids deep, 50 x 35 μm</td>
<td>20-25 tracheids deep, 30 x 15 μm</td>
</tr>
<tr>
<td>A. loharensis</td>
<td>Vagyan &amp; Raju 1981</td>
<td>Kamthi</td>
<td>24-72 tracheids deep, 47-58 μm</td>
<td>25 tracheids deep, 30-42 μm</td>
</tr>
<tr>
<td>A. mendozense</td>
<td>Maheshwari 1965</td>
<td>Raniganj</td>
<td>78 tracheids deep, 28 x 32 μm</td>
<td>2-3 tracheids deep, 23 x 11 μm</td>
</tr>
<tr>
<td>A. semibiseriatum</td>
<td>Pant &amp; Singh 1987</td>
<td>Raniganj</td>
<td>14-48 tracheids deep, 54-84 μm</td>
<td>1-3 tracheids deep, 54-67.5 x 20-34 μm, walls 20-34 μm</td>
</tr>
<tr>
<td>A. surangei</td>
<td>Agashe et al., 1981</td>
<td>Kamthi</td>
<td>25-95 tracheids deep, 30-60 x 61-67.5 μm, walls 18-21 μm</td>
<td>2-9 tracheids deep, 9-30 μm x 21-54 μm, walls 7-15 μm</td>
</tr>
<tr>
<td>A. veigaense</td>
<td>Agashe &amp; Kumar 1996</td>
<td>Kamthi</td>
<td>100-130 tracheids deep, 52 x 42.4 μm</td>
<td>5-15 tracheids deep, 32 x 20.5 μm</td>
</tr>
<tr>
<td>Arauxspiritys indicum</td>
<td>Pant &amp; Singh 1987</td>
<td>Raniganj</td>
<td>120-140 tracheids deep, 180 x 60 μm</td>
<td>2-4 tracheids deep, 60 x 30 μm</td>
</tr>
<tr>
<td>Australoxylon kallhargarense</td>
<td>Prasad &amp; Chandra 1978</td>
<td>Kamthi</td>
<td>70 tracheids deep, 32-59 x 22-50 μm, walls 5-18 μm</td>
<td>5-8 tracheids deep, 18-36 x 33-56 μm, walls 7-23 μm</td>
</tr>
<tr>
<td>Bairoxylon multiserial</td>
<td>Prasad &amp; Chandra 1981</td>
<td>Kamthi</td>
<td>5-7 mm wide growth ring, 25-5-42.5 μm</td>
<td>0</td>
</tr>
<tr>
<td>A. longicellularis</td>
<td>Prasad &amp; Chandra 1981</td>
<td>Kamthi</td>
<td>25-42.4 x 17-40 μm</td>
<td>5-6 tracheids deep, 15.3-17 μm</td>
</tr>
<tr>
<td>A. teixenae</td>
<td>Bajpai &amp; Maheshwari 1986</td>
<td>Raniganj</td>
<td>55-125 tracheids deep, 34-75 x 37-63 μm, walls 11-20 μm</td>
<td>1-2 tracheids deep</td>
</tr>
<tr>
<td>A. ranaensis</td>
<td>Pant &amp; Singh 1987</td>
<td>Raniganj</td>
<td>120-140 tracheids deep, 32 x 20.5 μm</td>
<td>3-8 tracheids deep, 14-34 x 47-72 μm, walls 7-18 μm</td>
</tr>
<tr>
<td>Barioxylon multiserial</td>
<td>Prasad 1986</td>
<td>Kamthi</td>
<td>2-7 tracheids deep, 10-12 x 28-82 μm, wall 12-15 μm</td>
<td>1-17 tracheids deep, 20 x 32 μm</td>
</tr>
<tr>
<td>Barakaroxylon jhariense</td>
<td>Surange &amp; Mathiy 1961</td>
<td>Barakar</td>
<td>35-60 tracheids deep, 38-60 x 70 μm, walls 10-18 μm</td>
<td>3-4 tracheids deep, 16-21 μm, walls 10-18 μm</td>
</tr>
<tr>
<td>B. monocanalosum</td>
<td>Kulkarni 1971</td>
<td>Barakar</td>
<td>45-55 tracheids deep, 21-31.5 μm</td>
<td>2-3 tracheids deep, 3.5-10.5 μm</td>
</tr>
<tr>
<td>Catervoxylon raniganjensis</td>
<td>Pant &amp; Singh 1987</td>
<td>Raniganj</td>
<td>25-130 tracheids deep, 29-105 x 24-27 μm, walls 4-13 μm</td>
<td>3-7 tracheids deep, 7-25 x 15-54 μm, walls 2-11 μm</td>
</tr>
<tr>
<td>Chapmaniaxylon raniganjensis</td>
<td>Pant &amp; Singh 1987</td>
<td>Raniganj</td>
<td>45-70 tracheids deep, 29-60 x 20-65 μm, walls 7-11 μm</td>
<td>2-7 tracheids deep, 5.33 x 21 x 54 μm, walls 3-9 μm</td>
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</table>
Dadoxylon adhariense  Prasad 1986  Kamthi
D. barakarensis  Surange & Saxena 1956  Barakar
D. chandrapurensis  Chitraley 1949  Kamthi
D. chandruariense  Prasad & Chandra 1979  Kamthi
D. jamuriense  Maheshwari 1965  Raniganj
D. maharashtraensis  Prasad & Chandra 1979  Kamthi
D. parenchymosum  Prasad & Chandra 1979  Kamthi
D. zaleskii  Sahni 1928  Raniganj
Domodaxylon lebekhinae  Bajpai & Maheshwari 1986  Raniganj

D. cf. waltsonii  Maheshwari 1963  Raniganj
Indooxylon canalousum  Surange & Maithy 1963  Barakar
Kamthioxylon adhariense  Mahabale & Vagany 1980  Kamthi
K. chandrapurensis  Agashe & Prasad 1989  Kamthi
Kooxylon pseudostratimodularis  Prasad 1986  Kamthi
K. mahabalei  Agashe & Prasad 1989  Kamthi
Kendoxylon fissilis  Pant & Singh 1987  Raniganj

Nandoroxylon sakensae  Biradar & Bonde 1981  Kamthi
Palaeoxylon heterocellularis  Prasad & Chandra 1980  Kamthi
Paracertextoxylon biseriatum  Pant & Singh 1987  Raniganj
P. raniganjensis  Pant & Singh 1987  Raniganj
Parapalaeospiroxylon burmundaensis  Pant & Singh 1987  Raniganj
Planoxylon indicum  Vagany & Mahabale 1974  Kamthi
Polysolenoxylon krauselii  Maheshwari 1972  Barakar
Protophyllocladoxylon indicum  Pant & Singh 1987  Raniganj

Prototaxipitys andrewsii  Agashe & Chitnis 1971  Kamthi
Prototaxipitys andrewsii  Agashe & Chitnis 1971  Kamthi
P. chandrapurensis  Agashe & Gowda 1981  Kamthi
P. gondwanense  Agashe et al., 1984  Barakar
P. uniseriale
P. maithyi  Prasad 1986  Kamthi
Ranaoxylon bengalensis  Pant & Singh 1987  Raniganj

Sclerospiroxylon marguerleri
Spyroxylon indicum  Prasad 1986  Kamthi
Mehta 1952  Barakar

48-88 μm x 36-83 μm, walls 7-14 μm
Present
30-40 tracheids deep, 57 x 74 μm
7 mm wide, 1-7 tracheids deep,
walls 5-6 μm
Rings clear, 13.6-23.8 x 39.1-42.5 μm
70-120 tracheids deep, 39-78
x 27-78 μm, walls 16-20 μm
17-18.7 x 20.4-34 μm
15.3-20 x 17-22 μm
Rings well marked
35-69 tracheids deep, 19.5-45.4
x 26-52 μm, walls 6.5 μm
25-51 x 18-36 μm, walls 5-6 μm
40-60 tracheids deep, 21-53 μm
63 tracheids deep, 57 x 58 μm
45-50 tracheids deep, 50 x 45 μm
34-47 x 52-65 μm
50-60 tracheids deep, 35 x 40 μm
10-70 tracheids deep, 45-104
x 29-63 μm, walls 12.27 μm
195-251 tracheids deep, 43 x 41 μm
60-110 tracheids deep.
20-24 x 48-60 μm
25-53 tracheids deep, 23-135 μm
x 14-77 μm, walls 3-11 μm
34-72 cells deep, 25-86
x 18-61 μm, walls 3-9 μm
35 tracheids, 50-70 x 30-70 μm,
walls 9-25 μm
114 tracheids deep, 48 x 72 μm
Rings 4-9 mm broad
28-50 racheteis, 36-4 x 30-70 μm,
absent
36-39 tracheids deep, 20-45 μm
95-130 tracheids deep, 35-45 μm
Growth rings distinct
absent
16-24 x 41-50 μm
44-56 x 24-55 μm
50-60 tracheids deep, 54-94
x 30-68 μm, walls 11-30 μm
Rings faint, 38 x 30-60 μm
23 μm
10-17 x 15-28 μm
3-7 cells deep, 16-21 x 25-30 μm
2-5 tracheids deep, 23-36 x 27-63 μm,
walls 18-32 μm
3-14 μm
<table>
<thead>
<tr>
<th>Taxa</th>
<th>Authors</th>
<th>Horizon</th>
<th>Early Wood</th>
<th>Late Wood</th>
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<tbody>
<tr>
<td>Taxopitys indica</td>
<td>Prasad &amp; Chandra 1978</td>
<td>Kamthi</td>
<td>80-110 tracheids deep,</td>
<td>3-5 tracheids deep, 10-16 x 21-24 μm</td>
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<tr>
<td>T. surangei</td>
<td>Prasad 1986</td>
<td>Kamthi</td>
<td>20-28 x 45-75 μm</td>
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<td>Trigonostrobus kamthiensis</td>
<td>Agashe &amp; Gowda 1981</td>
<td>Kamthi</td>
<td>3-5 tracheids deep, 28-47 x 35-53 μm</td>
<td>3-5 tracheids deep, 27-34 x 41-54 μm</td>
</tr>
<tr>
<td>Z. gondwanensis</td>
<td>Pant &amp; Singh 1987</td>
<td>Raniganj</td>
<td>120-175 tracheids deep, 35-54 μm</td>
<td>3-5 tracheids deep, 10-30 x 35-54 μm</td>
</tr>
<tr>
<td>Z. raniganjensis</td>
<td>Pant &amp; Singh 1987</td>
<td>Raniganj</td>
<td>50 tracheids deep, 36-83</td>
<td>4-6 tracheids deep, 14-36</td>
</tr>
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<td>Z. lepekhinae</td>
<td>Prasad &amp; Chandra 1979</td>
<td>Kamthi</td>
<td>x 25-64 μm, walls 7-20 μm</td>
<td>x 36-58 μm, walls 11-27 μm</td>
</tr>
<tr>
<td>Z. sorandensis</td>
<td>Prasad &amp; Chandra 1989</td>
<td>Kamthi</td>
<td>31-96 tracheids deep, 37-69</td>
<td>2-7 tracheids wide, 18-37</td>
</tr>
<tr>
<td>Z. simplexum</td>
<td>Chandra &amp; Prasad 1980</td>
<td>Kamthi</td>
<td>x 21-72 μm, walls 10-18 μm</td>
<td>x 21-51 μm, walls 12-18 μm</td>
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<td></td>
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<td></td>
<td>15-38 x 13-36-5 μm</td>
<td>Same as early wood</td>
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<td>120-130 tracheids deep, 45-55 μm</td>
<td>2-3 tracheids deep, 30-40 μm</td>
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<td></td>
<td></td>
<td>5-8 mm wide, 17-51 x 22-43 μm</td>
<td>Same as early wood</td>
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</table>

**TRIASSIC**

**JURASSIC**

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Authors</th>
<th>Horizon</th>
<th>Early Wood</th>
<th>Late Wood</th>
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<tbody>
<tr>
<td>Araucarioxyylon sp A</td>
<td>Sahni 1931</td>
<td>Maleri</td>
<td>55 μm</td>
<td>20 μm</td>
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<tr>
<td>Araucarioxyylon sp B</td>
<td>Sahni 1931</td>
<td>Tikii</td>
<td>50 μm</td>
<td>20 μm</td>
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<tr>
<td>Podocarpoxyylon malerianum</td>
<td>Sahni 1931</td>
<td>Maleri</td>
<td>Growth rings microscopically indistinct</td>
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</tr>
<tr>
<td>Podocarpoxyylon godavarianum</td>
<td>Sahni 1931</td>
<td>Maleri</td>
<td>Growth rings absent</td>
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</tr>
<tr>
<td>Araucarioxyylon parbhitaensis</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>24-42 tracheids deep, 35-98</td>
<td>3-5 tracheids deep, 14-30 x 16-40 μm</td>
</tr>
<tr>
<td>Araucarioxyylon samalense</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>x 56-78 μm, walls 16-24 μm</td>
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</tr>
<tr>
<td>Araucarioxyylon sp.</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>Growth rings distinct</td>
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<tr>
<td>Podocarpoxyylon rajmahalense</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>24-42 tracheids deep, 32-58</td>
<td>3-5 tracheids deep, 14-30 x 16-40 μm</td>
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<td>Podocarpoxyylon krauselii</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
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<tr>
<td>Podocarpoxyylon</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>cells 20-38 x 25-55 μm</td>
<td>cells 16-25 x 25-32 μm</td>
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<td>Taxaceoxyylon sahnii</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>20-38 x 25-55 μm</td>
<td>16-25 x 25-32 μm</td>
</tr>
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<td>Taxaceoxyylon sp. A</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>6-54 tracheids deep,</td>
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<td>Taxaceoxyylon sp. B</td>
<td>Rajanikanth &amp; Sukdev 1989</td>
<td>Kota</td>
<td>18-32 x 19-30 μm</td>
<td>—</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>26-56 x 34-66 μm</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>32-52 x 28-58 μm</td>
<td>17-28 μm</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>35-70 x 30-50 μm</td>
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### EARLY CRETACEOUS

<table>
<thead>
<tr>
<th>TAXA</th>
<th>AUTHORS</th>
<th>HORIZON</th>
<th>EARLY WOOD</th>
<th>LATE WOOD</th>
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<tbody>
<tr>
<td>Araucarioxylon rajmahalense</td>
<td>Sahni 1931</td>
<td>Rajmahal</td>
<td>cells 35-40 x 60-65 μm</td>
<td>cells 15 μm</td>
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<tr>
<td>Araucarioxylon jurassicum</td>
<td>Bharadwaj 1953</td>
<td>Rajmahal</td>
<td>cells 20-30 μm</td>
<td>cells 20-30 μm</td>
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<tr>
<td>Araucarioxylon amraparensi</td>
<td>Sah &amp; Jain 1964</td>
<td>Rajmahal</td>
<td>40-70 tracheids deep, 28-48 x 8-16 μm</td>
<td>—</td>
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<tr>
<td>Araucarioxylon mandroense</td>
<td>Sah &amp; Jain 1964</td>
<td>Rajmahal</td>
<td>cells 20-50 μm</td>
<td>—</td>
</tr>
<tr>
<td>Araucarioxylon santalense</td>
<td>Sah &amp; Jain 1964</td>
<td>Rajmahal</td>
<td>Indistinct</td>
<td>—</td>
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<td>Araucarioxylon bindrabunense</td>
<td>Sah &amp; Jain 1964</td>
<td>Rajmahal</td>
<td>Indistinct</td>
<td>—</td>
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<tr>
<td>Araucarioxylon agathoides</td>
<td>Krausel &amp; Jain 1964</td>
<td>Rajmahal</td>
<td>cells 31-48 μm</td>
<td>—</td>
</tr>
<tr>
<td>Araucarioxylon wynni</td>
<td>Borkar &amp; Bonde 1986</td>
<td>Kutch</td>
<td>cells 45 x 48 μm</td>
<td>1-3 cells deep,</td>
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<tr>
<td>Araucarioxylon amraparensi</td>
<td>Manik &amp; Srivastava 1991</td>
<td>Gangapur</td>
<td>85-105 cells deep, 40-60 x 30-40 μm</td>
<td>2-3 cells deep, 16-20 μm</td>
</tr>
<tr>
<td>Araucarioxylon rajivii</td>
<td>Jeyasingh &amp; Kumarasamy 1994</td>
<td>Sriperumbudur</td>
<td>30-40 tracheids wide, 35-45 x 65-95 μm</td>
<td>same as early wood</td>
</tr>
<tr>
<td>Araucarioxylon gibii</td>
<td>Jeyasingh &amp; Kumarasamy 1994</td>
<td>Sriperumbudur</td>
<td>30-50 tracheids deep, 45 x 60 μm</td>
<td>cells 10-15 μm</td>
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<td>Araucarioxylon mosurense</td>
<td>Jeyasingh &amp; Kumarasamy 1994</td>
<td>Sriperumbudur</td>
<td>210 tracheids deep, 12-66 x 65-95 μm</td>
<td>—</td>
</tr>
<tr>
<td>Baieroxyylon cicatricum</td>
<td>Muralidhara Rao &amp; Ramanujam 1986</td>
<td>Gangapur</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Platyspisroxylon parenchymatosum</td>
<td>Muralidhara Rao &amp; Ramanujam 1986</td>
<td>Gangapur</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Podocarpoxylon indicum</td>
<td>Bharadwaj 1953</td>
<td>Rajmahal</td>
<td>30-35 tracheids deep, 20-24 x 20-23 μm</td>
<td>5-6 cells deep, 20 x 12-15 μm</td>
</tr>
<tr>
<td>Podocarpoxylon rajmahalense</td>
<td>Jain 1965</td>
<td>Rajmahal</td>
<td>20-33 tracheids deep, 16-25 x 13-35 μm</td>
<td>walls 5-6 μm</td>
</tr>
<tr>
<td>Podocarpoxylon parthasarathi</td>
<td>Manik &amp; Srivastava 1991</td>
<td>Gangapur</td>
<td>20-50 tracheids deep, 42-50 x 28-40 μm</td>
<td>3-4 cells deep, 18 μm</td>
</tr>
<tr>
<td>Podocarpoxylon parthasarathi</td>
<td>Sahni 1931</td>
<td>Sriperumbudur</td>
<td>cells 30-40 μm</td>
<td>cells 10 μm</td>
</tr>
<tr>
<td>Podocarpoxylon tirumangalamense</td>
<td>Suryanarayana 1953</td>
<td>Sriperumbudur</td>
<td>cells 120-160 μm</td>
<td>cells 40-55 μm</td>
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<tr>
<td>Circoporoxylon amarjolense</td>
<td>Krausel &amp; Jain 1964</td>
<td>Rajmahal</td>
<td>10-40 tracheids deep.</td>
<td>—</td>
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<tr>
<td>Taxaceoxylon rajmahalense</td>
<td>Krausel &amp; Jain 1964</td>
<td>Rajmahal</td>
<td>20-40 tracheids deep, 17-30 x 10 μm</td>
<td>10 μm</td>
</tr>
<tr>
<td>Taxaceoxylon cupressoides</td>
<td>Sharma 1970</td>
<td>Rajmahal</td>
<td>25 x 30 μm</td>
<td>15 x 25 μm</td>
</tr>
<tr>
<td>Cupressinoxylon rajmahalense</td>
<td>Bharadwaj 1953</td>
<td>Rajmahal</td>
<td>25-30 tracheids deep, 26-28 x 36-40 μm</td>
<td>12-20 18-28 μm</td>
</tr>
<tr>
<td>Cupressinoxylon coromandelilim</td>
<td>Sahni 1931</td>
<td>Sriperumbudur</td>
<td>Growth rings well marked</td>
<td>—</td>
</tr>
<tr>
<td>Cupressinoxylon alternans</td>
<td>Sahni 1931</td>
<td>Raghavpuram</td>
<td>2-3 cells deep, 65-80 μm</td>
<td>2-3 cells deep, 120 μm</td>
</tr>
</tbody>
</table>

Fig. 2—Distribution and growth ring characteristics of Indian Gondwana woods.
conditions, restricted water availability, low wind velocity and low light intensity (Maheshwari et al., 1988).

The occurrence of distinct growth rings during Barakar times indicates definite seasons. Indian wood data from the Barakar Formation exhibit wide early wood, an average of 30-40 tracheids deep, and late wood 2-4 tracheids deep. Variations in the tracheidal cell sizes correspond to the different growth zones. Middle Permian wood data are wanting. Late Permian woods (Kamthi/Raniganj formations) from large trees with profuse branching and wide growth rings, indicate a markedly seasonal climate.

Tracheidal cell data show wide early wood, up to 70 cells deep, and narrow early wood, up to 25 cells deep. Abundant seasonal resource availability is evident from the large cellular sizes and draws support from the fact that the prevailing conditions also supported luxuriant growth of the Glossopteris flora. Lot of Gondwana Permian conifer-type wood is likely to represent glossopterids. Stable climates during the Permian allowed evolution of finer specialisations and adaptations because of the relative constancy of resources, which is also true for many recent ecosystems (Raghubanshi et al., 1991). Palaeocontinental positions too influence climatic regimes (King, 1958; Lele, 1977A, B; Rees et al., 1999).

**Triassic**

Petrified woods are scant in the Triassic sequence, except for sporadic reports of woods from the South Rewa and Pranhita-Godavari basins (Fig. 2). Woods resembling Araucariaceae and Podocarpaceae, represented by Araucarioxylon (2) and Podocarpoxyylon (2), have indistinct growth rings, indicating lack of definite seasons during the Triassic. The prevalence of a tropical arid climate during the Triassic times can be inferred on the presence of red beds and low plant diversity (Lele, 1974). Moreover non-availability of widespread plant fossil records restricts explicit climatic inferences. It was suggested that periodic deficiency of water supply resulted in impoverished plant growth. The paucity of wood fossils on Indian continent during the Triassic times is in consonant with other plant evidence.

**Jurassic**

The Jurassic wood flora is primarily known from the Kota Formation of the Pranhita-Godavari Graben (Fig. 2). Araucarioxylon, Podocarpoxyylon, Prototaxoxylon, Taxaceoxylon, Ginkgoxylon and Cupressinoxylon show an inconsistent distribution of growth rings, which may or may not be distinguishable, indicating local disturbances. Woods reported were of different stem diameters and had variable cell sizes and shapes, indicating variable climatic factors. Resource constraints and possible microenvironmental factors resulted in erratic growth ring features. Indian Jurassic woods show growth rings with 40 tracheidal cells deep in the early wood and 4 cells deep in the late wood with variable wall thickness.

**Early Cretaceous**

The Early Cretaceous wood taxa of India are distributed in the Rajmahal, Kutch, Pranhit-Godavari and Palar basins. Wood taxa belonging to five genera, Araucarioxylon, Baieroxylon, Platypteryxylon, Podocarpoxyylon, Taxaceoxylon, Circopoxylon and Cupressinoxylon and 23 species have been collected from different depositional regimes. Available data indicate inconsistency in the growth ring pattern, but most of the woods lack cellular details. Early wood tracheids are mostly 45 cells deep and late wood cells about 5 cells deep.

**ENVIRONMENTAL INTERPRETATIONS**

Since most of the wood genera discussed here represent unspecified gymnosperm taxa and are artificially defined, their bearing on explicit climatic inferences is somewhat tenuous. However, environmental factors like availability of sunlight, precipitation and nutrients are reflected in the tracheidal cell characters that form the basis of present synthesis. Since vegetation and soils are mirrors of the normal climates of a region, study of growth rhythms in fossil woods gives a glimpse of water/nutrient availability in the soil on which plants were growing.

Indian Permian Gondwana woods predominantly show growth rings, with distinct early and late woods. Woods of the Permian with distinct growth rings suggest favourable climatic conditions for the growth of trees, which contributed to the coal formation that was widespread at this time. Data available on Indian Permian Gondwana woods are in consonance with global data. Permian fossil woods known from Antarctica, South America, the Falkland Islands, Africa, Australia and India are not confidently assigned to any botanical family. Most of them are artificially defined genera and species. Presumably they all represent gymnosperms ([Pant & Singh, 1987 (India); Archangelsky, 1960; Maniero, 1951; Krausel & Doliangiti, 1958; Musa, 1978 (S. America); Maheshwari, 1972 (Antarctica); Krausel, 1928; Walton, 1925; Marguerier, 1973; Bamford & Philippe, 2001 (Africa); Sahni & Singh, 1926; Walkom, 1928 (Australia); Lepekhina & Yatsenko-Khmelevsky, 1966 (Falkland Islands)]. Growth ring features usually do not help in assigning to fossil wood to any particular family. At times features like pitting; or presence of tertiary spiral thickenings are suggestive of araucarian or taxinean affinity. Many of “conifer-like” woods in the Gondwana Permian probably belonged to glossopterids.

The absence of large structurally preserved logs in the Indian Mesozoic Gondwana is noteworthy. The occurrence of Podocarpaceae and Araucariaceae forests in Antarctica,
Australasia, southernmost South America and India during Early Cretaceous times is well established (Jefferson, 1982). Floras of southern continents from Queensland, Koonwara (Australia), Otway and Gippsland (Greater Artesian Basin, Australia), Hope Bay, Graham Land, Carapace Nunatak, Alexander Island, Antarctica are known for diverse gymnosperms. Wood types in the Mesozoic indicate a blind ending of evolutionary lines. Presumably ginkgos, corystosperms, peltasperms and others died out, as exemplified from the plant fossil records. Wood structures of recent southern hemisphere gymnosperms, particularly members of Araucariaceae and Podocarpaceae, are important components of Mesozoic floras. Similar wood affinities have been noted in South African Mesozoic florás (Schuze-Motel, 1966). Noticeable differences in floral compositions within the floras of particular basins can be attributed to preservational factors. This holds true for the Indian Mesozoic wood data. For example fossil woods known from the Rajmahal Formation show better preservation and also diversity since volcanic event helped to preserve nearby vegetation with little or no transport of material. Whereas in coastal basins the woods preserved are comparatively smaller in size and preserved in fluvial/paralic setup and transportation was much pronounced.

CONCLUSION

Highly seasonal conditions experienced at high latitudes can be inferred from the growth ring distribution of Permian woods. A moist, warm temperate climate can be conceived for the Late Permian, as evinced by large tree trunks with distinct growth rings; in addition, the association of coal supports the presence of water-rich conditions. The lack of distinct growth rings in the Triassic woods suggests an absence of seasonality. Available data on the Early Jurassic indicate an inconsistency in growth ring distribution and a lack of marked seasonal differentiation. The association of leaf fossils of Cycadales with conifers in the Early Jurassic suggests that the climate was no cooler than warm temperate. This is contrary to the reports of deciduous Cycadales of the \textit{Nilssonia} type in the high latitudes in the Northern Hemisphere in the Late Jurassic and Cretaceous. During the Early Cretaceous, conifer-dominated vegetation with wide growth rings in the secondary xylem indicates a warm climate with seasonal differentiation.

The general increase in mean ring width from Early to Late Gondwanan times indicates ameliorating climatic conditions, particularly benign summer conditions. The majority of fossil woods found in the Indian Gondwanan sediments are detached fragments of axes/stems. Big logs or \textit{in situ} trunks need to be recovered and worked out in detail to interpret long-term changes. The paucity of false growth rings suggests non-interruption of growth due to adverse conditions. Associations of various plant fossils preserved in the form of leaves, fructifications, seeds, pollen/spores, etc., belonging to Gymnosperms in various horizons of the Indian Gondwana offer a wide scope to work out environmental conditions at different times. Extensive collection of Gondwana fossil woods and their detailed study through an integrated approach incorporating quantitative vegetational physiognomy and sediment climate indicators are necessary.

It is also suggested that sometimes genetically controlled characters may be overshadowed by external environmental factors due to phenotypic plasticity (Lev A Zhivotovsky, 1997). On the other hand in plants growing in similar environmental conditions genetic variations may overrule environmental effects (Creber & Chaloner, 1984b). In the high southern latitudes during times of glaciation strong growth rings are present, as in the Permian photoperiodic factors and temperature dictated growth ring formation and seasonal variations. Subsequently in the Mesozoic growth rings were not strong, micro environmental and genetic factors may have played a key role (Ash & Creber, 1992).

Structural variability of wood from different parts of individual trees leads to complications in the classification of fossil material that demand a careful study (Lepekhina, 1972). Rapid burial (petrifaction) of trees allows best preservation of growing season markers. Growth ring analysis indicates seasonality, climatic sensitivity, and growth rate (Jefferson, 1982). It is suggested that continental margins generally show moderate to extreme seasonality (Barron & Washington, 1982). Gondwana woods of India, which were from a relatively coastal part of Gondwanaland, usually show growth rings, since growing conditions leave visible effects. In the absence of contemporary meteorological data during Gondwana times on what is now on the Indian continent, fossil woods constitute an important tool for understanding the past impact of climate on tree growth.

Most of the earlier workers concentrated on the taxonomy and description of fossil woods and made no concerted efforts to understand the implications of variations in wood structure in interpreting palaeoclimate. Thus it has become imperative to synthesise available data to deduce possible environmental influences. Factors like fossil wood position-to which part of the plant it belonged, preservation constraints, habitat considerations, coastal/continental and other related factors were not considered in earlier characters that reflect environmental changes-age of rings (young/mature), mean ring width, mean number of cells per ring, frequency of narrow rings, late wood width, occurrence of false rings, traumatic parenchyma, mean tracheid diameter, tracheid unit length etc.-throw much light on past environmental changes. It is high time that botanists, ecologists, geologists, meteorologists, foresters and associated workers should come together to do an integrative study of past plant-climate interactions. Factors like landslides, glaciations, erosion cycles and other physical happenings can be better understood through an understanding of plant architecture/engineering. The relative
latitudinal positions of different Gondwanan areas at different times during the drift of the southern landmass presumably influenced climatic regimes and consequent floral changes (Rees et al., 1999; Ziegler et al., 1983). Palaeophysiographic conditions of the landscape during Gondwanan times supported varied types of plant growth, and climatic fluctuations were archived in the cellular structures. A synthetic process of reasoning that draws on all lines of evidence such as palaeosols, leaf physiognomy and climate modelling, is lacking for the Indian Gondwanan. Contradictory inferences based on sedimentology and growth ring data demand a multidisciplinary approach. As Birbal Sahni (1936) remarked “in this age of specialization which inevitably tends to confine thought in compartments, one is apt to overlook or to underrate bearings of one branch of science upon another”

- Fossil tree ring studies need a new thrust.

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REFERENCES


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