

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

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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-latitude 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 काष्ठ अध्ययन की पर्यावरणीय युगपत् अन्तर्वृद्धि

अन्नमराजु रजनीकान्त एवं रजनी तिवारी

सारांश

भारत के विभिन्न गोंडवाना द्रोणियों से प्राप्त अनावृतबीजी काष्ठ जीवाश्म के अभिलेखों का संश्लेषण प्रदर्शित किया गया है तथा द्वितीयक काष्ठ में वृद्धि वलय के लक्षण (विशेषकर वाहिनिकीय कोशिका लक्षण) संभावी पुराजलवायविक संकेत हेतु मूल्यांकन किया गया है। परमियन काष्ठ जीवाश्म अधिकतर दामुदा, वर्धा तथा प्राणहिता-गोदावरी द्रोणियों से अभिलिखित किए गए हैं। इनकी कई प्रजातियों में सामान्यतः वृद्धि वलय होती है तथा मजबूत ऋतुनिष्ठ होने का सुझाव देती है। दक्षिण रीवा गोंडवाना द्रोणी से ट्रायसिक काष्ठों की अत्यल्प जानकारी है। वृद्धि वलयों की कमी अस्पष्ट मौसम विभेद का संकेत करती है। प्राणहिता-गोदावरी द्रोणिका से प्राप्त जुरासिक काष्ठों पर उपलब्ध प्रमाण वृद्धि वलय वितरण में एकरूपता की कमी का संकेत करते हैं। दामुदा, प्राणहिता-गोदावरी, पूर्व-तटीय एवं कच्छ द्रोणियों से अभिलिखित प्रारम्भिक क्रिटेशस काष्ठ जीवाश्म अधिकतर वृद्धि वलय प्रदर्शित करते हैं जो कि पृथक मौसमों की व्यापकता सुझाते हैं। भारतीय

गोंडवाना काष्ठों में काष्ठ संचय संभवतः पारिस्थितिकीय कारकों एवं समलक्षणीय सुघटयता पर आधारित था जिसके अन्तर्गत पर्यावरणीय अंतर (आनुवंशिक लचक) के आधार पर समजीवी से भिन्नता एक प्रमुख कारक था। यद्यपि पुराअक्षांशीय एवं पुराभूआकृतिकी प्रतिबंधों ने आवास तथा परवर्ती जैवसादकीय क्रियाओं को प्रभावित किया जिसके कारण पुराजलवायु संबंधी ज्ञान अपूर्ण रहा।

संकेत शब्द—काष्ठ, गोंडवाना, पुराजलवायु, वृद्धि बलय, मौसम.

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 fluvio-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 & Bandyopadhyay, 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 out numbered 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

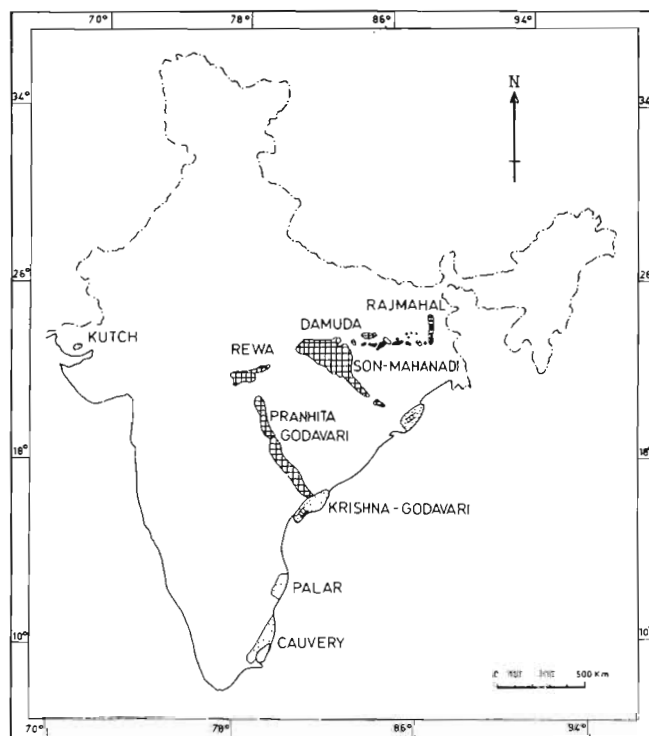


Fig. 1—Sedimentary basins of Gondwana wood occurrence.

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 & Lorsehehe, 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 (Fritzhans, 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: floras 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

TAXA	AUTHORS	HORIZON	EARLY WOOD	LATE WOOD
<i>Agathioxylon vestunanense</i>	Agashe & Prasad 1989	Kamthi	120-130 tracheids deep, 45-66 µm	3-5 tracheids deep, 20-30 µm
<i>A. zaranense</i>	Agashe & Prasad 1989	Kamthi	110-120 tracheids deep, 65 µm	3-6 tracheids deep, 40-50 µm
<i>Araucarioxylon bengalense</i>	Mareshwari 1972	Barakar	1.5-6.5 mm deep, 25-45 x 25-44 µm	5-7 tracheids deep, 14-25 µm, walls 7 µm
<i>A. bhivkmdense</i>	Agashe & Prasad 1989	Kamthi	120-130 tracheids deep, 60 x 30 µm	2-4 tracheids deep, 30 x 2 µm
<i>A. bradshawianum</i>	Bajpai & Maheshwari 1986	Raniganj	60-75 tracheids deep, 26-52 x 32.5-52 µm, walls 13-19 µm	4-5 tracheids deep, 13-19.5 x 26-52 µm, walls 13-19.5 µm
<i>A. gondwanense</i>	Maheshwari 1972	Barakar	40-50 tracheids deep, 35-70 µm	17-28 µm, wall 9-28 µm
<i>A. kharkhariense</i>	Maheshwari 1972	Barakar	40-70 tracheids deep, 42-56 µm	2-3 tracheids deep, walls 15-28 µm
<i>A. kolhariensis</i>	Agashe & Prasad 1983	Kamthi	70-80 tracheids deep, 50 x 40 µm	30 x 20 µm
<i>A. kumarpurensis</i>	Bajpai & Singh 1986	Raniganj	44-79 x 31-63 µm, walls 9-24 µm	11-32 x 31-48 µm, walls 7-17 µm
<i>A. lathiense</i>	Agashe <i>et al.</i> , 1981	Kamthi	150-160 tracheids deep, 50 x 35 µm	20-25 tracheids deep, 30 x 15 µm
<i>A. loharensis</i>	Agashe & Gowda 1978	Kamthi	24-72 tracheids deep, 47-58 µm	25 tracheids deep, 30-42 µm
<i>A. nandorii</i>	Vagyant & Raju 1981	Kamthi	78 tracheids deep, 28 x 32 µm	2-3 tracheids deep, 23 x 11 µm
<i>A. ningahense</i>	Maheshwari 1965	Raniganj	14-48 tracheids deep, 54-84 x 61-67.5 µm, walls 18-21 µm	1-3 tracheids deep, 54-67.5 x 20-34 µm, walls 20-34 µm
<i>A. semibiseriatum</i>	Pant & Singh 1987	Raniganj	25-95 tracheids deep, 30-60 x 30-62 µm, walls 3-11 µm	2-9 tracheids deep, 9-30 µm x 21-54 µm, walls 7-15 µm
<i>A. surangei</i>	Agashe <i>et al.</i> , 1981	Kamthi	100-130 tracheids deep, 52 x 42.4 µm	5-15 tracheids deep, 32 x 20.5 µm
<i>A. wejgaense</i>	Agashe & Kumar 1996	Kamthi	120-140 tracheids deep, 180 x 60 µm	2-4 tracheids deep, 60 x 30 µm
<i>Araucarioxylon indicum</i>	Pant & Singh 1987	Raniganj	70 tracheids deep, 32-59 x 22-50 µm, walls 5-18 µm	5-8 tracheids deep, 18-36 x 33-56 µm, walls 7-23 µm
<i>Australoxylon kanthargarensis</i>	Prasad & Chandra 1978	Kamthi	5-7 mm wide growth ring, 25.5-42.5 x 20.4-47 µm	—
<i>A. longicellularis</i>	Prasad & Chandra 1981	Kamthi	25-42.4 x 17-40 µm	5-6 tracheids deep, 15.3-17 µm
<i>A. teixei</i>	Bajpai & Maheshwari 1986	Raniganj	—	1-2 tracheids deep
<i>A. ranaensis</i>	Pant & Singh 1987	Raniganj	55-125 tracheids deep, 34-75 x 37-63 µm, walls 11-20 µm	3-8 tracheids deep, 14-34 x 47-72 µm, walls 7-18 µm
<i>Bairoxylon multiserialle</i>	Prasad 1986	Kamthi	2-7 tracheids deep, 10-12 x 28-82 µm wall 12-15 µm	1-17 tracheids deep, 20 x 32 µm
<i>Barakaroxylon jhariense</i>	Surange & Maithy 1961	Barakar	35-60 tracheids deep, 38-60 x 70 µm, walls 10-18 µm	3-4 tracheids deep, 16-21 µm, walls 10-18 µm
<i>B. monocanalosum</i>	Kulkarni 1971	Barakar	45-55 tracheids deep, 21-31.5 µm	2-3 tracheids deep, 3.5-10.5 µm
<i>Cateroxylon raniganjensis</i>	Pant & Singh 1987	Raniganj	25-130 tracheids deep, 29-105 x 24-27 µm, walls 4-13 µm	3-7 tracheids deep, 7-25 x 15-54 µm, walls 2-11 µm
<i>Chapmanoxylon raniganjensis</i>	Pant & Singh 1987	Raniganj	45-70 tracheids deep, 29-60 x 20-65 µm, walls 7-11 µm	2-7 tracheids deep, 5-33 µm x 21 x 54 µm, walls 3-9 µm
<i>C. indicum</i>	Pant & Singh 1987	Raniganj	12-70 tracheids deep,	1-8 tracheids deep, 18-36 x 32-62 µm,

<i>Dadoxylon adhariense</i>	Prasad 1986	Kamthi	48-88 µm x 36-83 µm, walls 7-14 µm	walls 17 x 18 µm
<i>D. barakarensis</i>	Surange & Saxena 1956	Barakar	Present	—
<i>D. chandensis</i>	Chitale 1949	Kamthi	30-40 tracheids deep, 57 x 74 µm	7-8 tracheids deep, 39 x 18 µm
			7 mm wide, 1-7 tracheids deep, walls 5-6 µm	1.22 mm wide
<i>D. chandrapurensis</i>	Prasad & Chandra 1979	Kamthi	Rings clear, 13.6-23.8 x 39.1-42.5 µm	—
<i>D. januriense</i>	Maheshwari 1965	Raniganj	70-120 tracheids deep, 39-78 x 27-78 µm, walls 16-20 µm	1-3 tracheids deep, 30-40 µm
			17-18.7 x 20.4-34 µm	—
<i>D. maharashtraensis</i>	Prasad & Chandra 1979	Kamthi	17-18.7 x 51-64.7 µm	15.3-20 x 17-22 µm
<i>D. parenchymosum</i>	Prasad & Chandra 1979	Kamthi	Rings well marked	—
<i>D. zaleskvi</i>	Sahni 1928	Raniganj	35-69 tracheids deep, 19.5-45.4 x 26-52 µm, walls 6.5 µm	1-4 tracheids deep, 13-15 x 32.5-39 µm, walls 6.5
<i>Damudoxylon lepekhinae</i>	Bajpai & Maheshwari 1986	Raniganj	25-51 x 18-36 µm, walls 5-6 µm	15-22 µm, walls 5-6 µm
			40-60 tracheids deep, 21-53 µm	2-4 tracheids deep, 10-21 µm, walls 10-21 µm
<i>D. cf. waltonii</i>	Maheshwari 1967	Raniganj	63 tracheids deep, 57 x 58 µm	2-3 tracheids deep, 48 x 24 µm
<i>Indoxylon canulosum</i>	Surange & Maithy 1963	Barakar	45-50 tracheids deep, 50 x 45 µm	2-3 tracheids deep, 35 x 20 µm
<i>Kamthioxylon adhariense</i>	Mahabale & Vagyan 1980	Kamthi	34-47 x 52-65 µm	10-12 tracheids deep, 27-34 x 41-54 µm
<i>K. chandrapurensis</i>	Agashe & Prasad 1989	Kamthi	50-60 tracheids deep, 35 x 40 µm	2-3 tracheids deep, 35-40 x 25-30 µm
<i>Kaokoxylon pseudotrimedullaris</i>	Prasad 1986	Kamthi	10-70 tracheids deep, 45-104 x 29-63 µm, walls 12-27 µm	3-8 tracheids deep, 9-21 x 27-52, walls 5-11 µm
<i>K. mahabalei</i>	Agashe & Prasad 1989	Kamthi	195-251 tracheids deep, 43 x 41 µm	1-5 tracheids deep, 19 x 40 µm
<i>Kendoxylon fissilis</i>	Pant & Singh 1987	Raniganj	60-110 tracheids deep, 20-24 x 48-60 µm	4-8 tracheids deep, 14-16 x 12-24 µm
<i>Nandoroxyton saksenae</i>	Biradar & Bonde 1981	Kamthi	25-53 tracheids deep, 23-135 µm	4-8 tracheids deep, 7-27 x 14-56 µm, walls 3-9 µm
<i>Palaeospiroxylon heterocellularis</i>	Prasad & Chandra 1980	Kamthi	x 14-77 µm, walls 3-11 µm	3-9 tracheids deep, 11-27 x 20-27 µm, walls 3-16 µm
			34-72 cells deep, 25-86 x 18-61 µm, walls 3-9 µm	5 tracheids deep, 27-47 x 38-61 µm, walls 14-29 µm
<i>Paracateroxyton biserialatum</i>	Pant & Singh 1987	Raniganj	35 tracheids, 50-70 x 30-70 µm, walls 9-25 µm	2-3 tracheids deep, 40 x 16 µm
			114 tracheids deep, 48 x 72 µm	—
<i>P. raniganjensis</i>	Pant & Singh 1987	Raniganj	Rings 4-9 mm broad	2-5 tracheids deep, 16-39 x 34-61 µm, walls 11-22 µm
<i>Parapalaeospiroxylon burmundiaensis</i>	Pant & Singh 1987	Raniganj	28-50 tracheids, 36-4 x 30-70 µm,	absent
<i>Planoxylon indicum</i>	Vagyan & Mahabale 1974	Kamthi	absent	3-7 tracheids deep, 5.5 µm
<i>Polysolenoxylon krauselli</i>	Maheshwari 1972	Barakar	36-39 tracheids deep, 20-45 µm	4-6 tracheids deep, 20-25 µm
<i>Protophyllocladoxylon indicum</i>	Pant & Singh 1987	Raniganj	95-130 tracheids deep, 35-45 µm	—
			Growth rings distinct	10-17 x 15-28 µm
<i>Prototaxopitys andrewsii</i>	Agashe & Chitnis 1971	Kamthi	16-24 x 41-50 µm	3-7 cells deep, 16-21 x 25-30 µm
<i>Prototaxoxylon andrewsii</i>	Agashe & Chitnis 1971	Kamthi	44-56 x 24-55 µm	2-5 tracheids deep, 23-36 x 27-63 µm, walls 18-32 µm
<i>P. chandrapurensis</i>	Agashe & Gowda 1981	Kamthi	50-60 tracheids deep, 54-94 x 30-68 µm, walls 11-30 µm	—
<i>P. gondwanense</i>	Agashe <i>et al.</i> , 1984	Barakar	Rings faint, 38 x 30-60 µm	3-14 µm
			23 µm	
<i>P. uniseriale</i>	Prasad 1986	Kamthi		
<i>P. maithyi</i>	Prasad 1986	Kamthi		
<i>Ranaoxylon bengalensis</i>	Pant & Singh 1987	Raniganj		
<i>Sclerospiroxylon margueritae</i>	Prasad 1986	Kamthi		
<i>Spiroxylon indicum</i>	Mehta 1952	Barakar		

<i>Taxopitys indica</i>	Prasad & Chandra 1978	Kamthi	80-110 tracheids deep, 20-28 x 45-75 µm	3-5 tracheids deep, 10-16 x 21-24 µm
<i>T. surangei</i>	Prasad 1986	Kamthi	Rings faint, 21-51 x 30-58 µm	—
<i>Trigonomyelon kamthiensis</i>	Prasad 1986	Kamthi	3-5 tracheids deep, 28-47 x 35-53 µm	3-5 tracheids deep, 27-34 x 41-54 µm
<i>Zallessioxylon barakarensis</i>	Agashe & Gowda 1981	Kamthi	120-175 tracheids deep, 35-54 µm	3-5 tracheids deep, 10-30 x 35-54 µm
<i>Z. gondwanensis</i>	Pant & Singh 1987	Raniganj	50 tracheids deep, 36-83 x 25-64 µm, walls 7-20 µm	4-6 tracheids deep, 14-36 x 36-58 µm, walls 11-27 µm
<i>Z. raniganjensis</i>	Pant & Singh 1987	Raniganj	11-96 tracheids deep, 37-69 x 21-72 µm, walls 10-18 µm	2-7 tracheids wide, 18-37 x 21-51 µm, walls 12-18 µm
<i>Z. lepekhinae</i>	Chandra & Prasad 1979	Kamthi	15-38 x 13.6-38.5 µm	Same as early wood
<i>Z. sarandensis</i>	Agashe & Prasad 1989	Kamthi	120-130 tracheids deep, 45-55 µm	2-3 tracheids deep, 30-40 µm
<i>Z. simplexum</i>	Chandra & Prasad 1980	Kamthi	5-8 mm wide, 17-51 x 22-43 µm	Same as early wood

TRIASSIC

TAXA	AUTHORS	HORIZON	EARLY WOOD	LATE WOOD
<i>Araucarioxylon sp A</i>	Sahni 1931	Maleri	55 µm	20 µm
<i>Araucarioxylon sp B</i>	Sahni 1931	Tikki	50 µm	20 µm
<i>Podocarpoxylon malerianum</i>	Sahni 1931	Maleri	Growth rings microscopically indistinct	—
<i>Podocarpoxylon godavarianum</i>	Sahni 1931	Maleri	Growth rings absent	—

JURASSIC

TAXA	AUTHORS	HORIZON	EARLY WOOD	LATE WOOD
<i>Araucarioxylon pranhitensis</i>	Rajamikanth & Sukhdev 1989	Kota	24-42 tracheids deep, 35-98 x 56-78 µm, walls 16-24 µm	3-5 tracheids deep, 14-30 x 16-40 µm
<i>Araucarioxylon santalense</i>	Rajamikanth & Sukhdev 1989	Kota	Growth rings distinct	—
<i>Araucarioxylon sp.</i>	Rajamikanth & Sukhdev 1989	Kota	24-42 tracheids deep, 32-58 x 56-78 µm, walls 16-24 µm	3-5 tracheids deep, 14-30 x 16-40 µm
<i>Podocarpoxylon rajmahalense</i>	Rajamikanth & Sukhdev 1989	Kota	cells 20-38 x 25-55 µm	cells 16-25 x 25-32 µm
<i>Podocarpoxylon krauselii</i>	Rajamikanth & Sukhdev 1989	Kota	20-38 x 25-55 µm	16-25 x 25-32 µm
<i>Podocarpoxylon</i> <i>chandrapurensis</i>	Rajamikanth & Sukhdev 1989	Kota	6-54 tracheids deep, 18-32 x 19-30 µm	—
<i>Taxaceoxylon sahnii</i>	Rajamikanth & Sukhdev 1989	Kota	26-56 x 34-66 µm	—
<i>Taxaceoxylon sp. A</i>	Rajamikanth & Sukhdev 1989	Kota	32-52 x 28-58 µm	17-28 µm
<i>Taxaceoxylon sp. B</i>	Rajamikanth & Sukhdev 1989	Kota	35-70 x 30-50 µm	—

Ginkgoxylon divitii Biradar & Mahabale 1978 Kota 21-24 x 34-40 µm 1-4 tracheids deep, 14 x 29 µm
Cupressinoxylon kotacense Rajanikanth & Sukhdev 1989 Kota 24-52 x 28-54 µm —
Prototaxoxylon liassicum Muralidhara Rao 1991 Kota —

EARLY CRETACEOUS

TAXA	AUTHORS	HORIZON	EARLY WOOD	LATE WOOD
<i>Araucarioxylon rajmahalense</i>	Sahni 1931	Rajmahal	cells 35-40 x 60-65 µm	cells 15 µm
<i>Araucarioxylon jurassicum</i>	Bharadwaj 1953	Rajmahal	cells 20-30 µm	cells 20-30 µm
<i>Araucarioxylon anraparensis</i>	Sah & Jain 1964	Rajmahal	40-70 tracheids deep, 28-48 x 8-16 µm	—
<i>Araucarioxylon mandroense</i>	Sah & Jain 1964	Rajmahal	cells 20-50 µm	—
<i>Araucarioxylon santalense</i>	Sah & Jain 1964	Rajmahal	Indistinct	—
<i>Araucarioxylon bindrabunense</i>	Sah & Jain 1964	Rajmahal	Indistinct	—
<i>Araucarioxylon agathoides</i>	Krausel & Jain 1964	Rajmahal	cells 31-48 µm	—
<i>Araucarioxylon wynnii</i>	Borkar & Bonde 1986	Kutch	cells 45 x 48 µm	1-3 cells deep,
<i>Araucarioxylon anraparensis</i>	Manik & Srivastava 1991	Gangapur	85-105 cells deep, 40-60 x 30-40 µm	2-3 cells deep, 16-20 µm
<i>Araucarioxylon rajvii</i>	Jeyasingh & Kumarasamy 1994	Sriperumbudur	30-40 tracheids wide, 35-45 x 65-95 µm	same as early wood
<i>Araucarioxylon giftii</i>	Jeyasingh & Kumarasamy 1994	Sriperumbudur	30-50 tracheids deep, 45 x 60 µm	cells 10-15 µm
<i>Araucarioxylon mosturensis</i>	Jeyasingh & Kumarasamy 1994	Sriperumbudur	210 tracheids deep, 12-66 x 65-95 µm	—
<i>Baieroxylon cicatricium</i>	Muralidhara Rao & Ramanujam 1986	Gangapur	—	—
<i>Platyspiroxylon parenchymatosum</i>	Muralidhara Rao & Ramanujam 1986	Gangapur	—	—
<i>Podocarpoxylon indicum</i>	Bharadwaj 1953	Rajmahal	30-35 tracheids deep, 20-24 x 20-23 µm	5-6 cells deep, 20 x 12-15 µm walls 5-6 µm
<i>Podocarpoxylon rajmahalense</i>	Jain 1965	Rajmahal	20-33 tracheids deep,	16-25 x 13-35 µm
<i>Podocarpoxylon parithasarathi</i>	Manik & Srivastava 1991	Gangapur	20-50 tracheids deep, 42-50 x 28-40 µm	3-4 cells deep, 18 µm
<i>Podocarpoxylon parithasarathi</i>	Sahni 1931	Sriperumbudur	cells 30-40 µm	cells 10 µm
<i>Podocarpoxylon tirumangalense</i>	Suryanarayana 1953	Sriperumbudur	cells 120-160 µm	cells 40-55 µm
<i>Circoporoxylon amarjolense</i>	Krausel & Jain 1964	Rajmahal	10-40 tracheids deep,	—
<i>Taxaceoxylon rajmahalense</i>	Krausel & Jain 1964	Rajmahal	20-40 tracheids deep, 17-30 x 10 µm	10 µm
<i>Taxaceoxylon cupressoides</i>	Sharma 1970	Rajmahal	25 x 30 µm	15 x 25 µm
<i>Cupressinoxylon rajmahalense</i>	Bharadwaj 1953	Rajmahal	25-30 tracheids deep, 26-28 x 36-40 µm	12-20 18-28 µm
<i>Cupressinoxylon coromandelinum</i>	Sahni 1931	Sriperumbudur	Growth rings well marked	—
<i>Cupressinoxylon alternans</i>	Sahni 1931	Raghavapuram	2-3 cells deep, 65-80 µm	2-3 cells deep, 120 µm

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 *Podocarpoxyton* (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 consonance with other plant evidence.

Jurassic

The Jurassic wood flora is primarily known from the Kota Formation of the Pranhita-Godavari Graben (Fig. 2). *Araucarioxylon*, *Podocarpoxyton*, *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, Pranhita-Godavari and Palar basins. Wood taxa belonging to five genera, *Araucarioxylon*, *Baieroxylon*, *Platyspiroxylon*, *Podocarpoxyton*, *Taxaceoxylon*, *Circoporoxylon* 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 & Dolianiti, 1958; Mussa, 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 floras (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 *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 *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 (petrification) 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). Palaeophysiological 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 Gondwana. 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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