1. Physiognomy and phytosociology of the international woodlands research sites*

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Contents

The advent of the International Biological Programme led to a large number of cooperative ecosystem studies that would not have flourished in another milieu. Ecologists throughout the world, eventually from more than 60 nations, agreed to investigate ecosystem structure and function in both native and managed systems in ways that they hoped would permit refined comparison and, eventually, global synthesis. The juxtaposition of the various land masses comprising the circumpolar arctic Tundra led to early comparisons and international cooperation (Wielgolaski & Rosswall, 1971; Bliss & Wielgolaski, 1973; Wielgolaski, 1975*ab*), although the rigors of the arctic environment necessarily limited the number of study sites. Grasslands and deserts received extensive treatment (Orians & Solbrig, 1977; Simpson, 1977; Mabry, Hunziker & Difeo, 1977; Innis, 1978), as did Mediterranean ecosystems, (di Castri & Mooney, 1973; Mooney, 1977). A combination of low populations of scientists and location in an array of developing nations again limited the number of participating grassland and desert sites.

The vast temperate and boreal regions of the earth, heavily concentrated in the northern hemisphere, have long harbored the population centers of the world. In these regions, too, the great universities and centers of research have developed. Consequently, the northern forests of the globe

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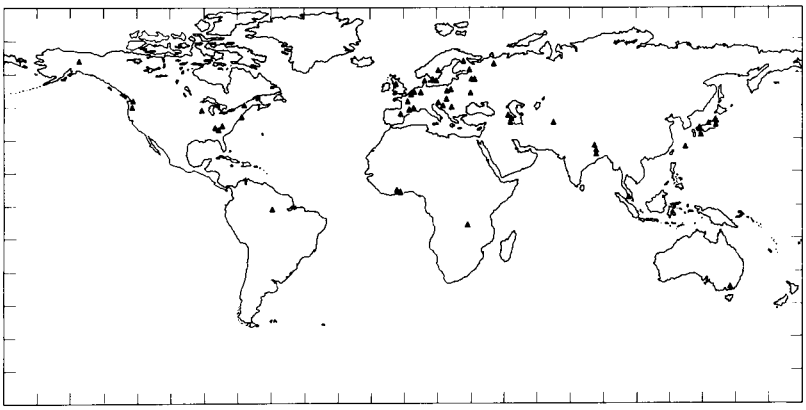

Fig. 1.1. The distribution of research sites in the International Woodlands Data Set (IBP). Each symbol may indicate more than one field site. Projection is Smithsonian Standard Earth II.

have been well-studied relative to other vegetation types, and the impetus of the IBP built an ecosystem edifice on an already appreciable foundation of knowledge (Reichle, 1970; Reichle, Franklin & Goodall, 1975). Scientists from 23 countries have now contributed to the IBP Woodlands Data Set, with information from 117 study sites (Fig. 1.1). These data, available in computerized form at Oak Ridge National Laboratory, now permit a suite of quantitative analyses, many of which appear elsewhere in this volume.

The purpose of this chapter, however, is to describe and qualitatively compare the forests studied as a result of the IBP. While interaction among scientists has continually expanded internationally, many ecologists have never had the opportunity to appreciate the great Douglas fir forests of the Pacific northwest in the United States, the magnificent beech forests of Europe, or the impressive Japanese *Cryptomeria* communities. Thus, it is important that an introduction to the breadth of the forest systems represented in the IBP be undertaken. While it is not possible to treat each site in depth, broad classes of forests can be characterized, and both the physiognomy and the phytosociology can be discussed solely on the basis of the Woodlands Data Set (see Chapter 11).

Classification system

In attempting to analyze and compare a large array of forest ecosystems, a degree of stratification is a prerequisite. In order to provide a working classification that would serve the 117 sites of the Woodlands Data Set, a variety of existing classification schemes were examined, including those of Braun-Blanquet (1932), Fosberg (1967), UNESCO (1973) and Ellenberg & Mueller-Dombois (1975). While each of these had useful features, none

Table 1.1. *Site number, name, forest type, and overstory composition of ecosystems in the International Woodlands Data Set. Forests have been delineated by climate (Tr, tropical; M, Mediterranean; Te, temperate; Bo, Boreal), life-form (BL, broad-leaved; NL, needle-leaved), behavior (D, deciduous; E, evergreen), and status (natural is assumed; plantation indicated by /P). (Adapted from DeAngelis* et al., 1978)

Site no.	Name	Forest type	Principal overstory components
1	Mt Disappointment, Australia	MBLE	*Eucalyptus obliqua*
2	Virelles, Belgium	TeBLD	*Quercus robur, Carpinus betulus, Fagus sylvatica, Acer campestris, Prunus avium*
3	Manaus, Brazil	TrBLE	Leguminosae, Sapotaceae, Lauraceae, Palmae, Annonaceae, Lecythidaceae, Rubiaceae, Burseraceae
4–7	Ontario site region 5, Canada	BoNLE	*Picea rubens, P. mariana, P. glauca, Pinus strobus, Abies balsamea, Tsuga canadensis, Thuja occidentalis*
8	Bab, Czechoslovakia	TeBLD	*Carpinus betulus, Acer campestris, Quercus cerris, Quercus petraea, Cornus mas, Crataegus oxyacantha, Ulmus carpinifolia*
9	Hestehaven, Denmark	TeBLD	*Fagus sylvatica*
10	Oulu, Finland	BoNLE	*Picea excelsa*
11	Fontainebleau, France	TeBLD	*Fagus sylvatica*
12	Madeleine, France	MBLD	*Quercus ilex*
13	Rouquet, France	MBLD	*Quercus ilex*
14	Sikfokut, Hungary	TeBLD	*Quercus petraea, Quercus cerris*
15–16	Chakia Forest, Varanasi, India	TrBLD	*Shorea robusta, Buchanania lanzan*
17	Chakia, India	TrBLD	*Shorea robusta, Buchanania lanzan, Anogeissus latifolia, Terminalia tomentosa*
18–23 and 30–35	Sal Plantation Gorakhpur Forest Division, India	TrBLD/P	*Shorea robusta*
24–29	Teak Plantation Gorakhpur Forest Division, India	TrBLD/P	*Tectona grandis*
36	Banco (plateau), Ivory Coast	TrBLE	*Turraeanthus africana, Dacryodes klaineana, Strombosia glaucescens, Berlinia confusa, Coula edulis, Chrysophyllum sp., Combretodendron africanum, Allanblackia floribunda*

(*Table* 1.1 *continued*)

Site no.	Name	Forest type	Principal overstory components
37	Yapo, Ivory Coast	TrBLE	*Dacryodes klaineana, Allanblackia floribunda, Coula edulis, Strombosia glaucescens, Scottelia chevalieri, Scytopetalum thieghemii, Piptadeniastrum africanum, Tarrietia utilis*
38	JPTF–66–Koiwai, Japan	TeNLD/P	*Larix leptolepis*
39	Ashu, Kyoto, Japan	TeBLD	*Fagus crenata, Carpinus laxiflora, Quercus mongolica*
40	Okinawa, Japan	TeBLE	*Castanopsis cuspidata*
41	JPTF–Okita, Okita, Japan	TeNLE	*Pinus densiflora*
42	Shigayama, Japan	TeNLE	*Tsuga diversifolia, Abies mariesii, Betula ermani*
43	JPTF–70 Yusuhara Kubotaniyama, Japan	TeNLE	*Tsuga sieboldii, Chamaecyparis obtusa, Pinus densiflora*
44	JPTF–71 Yusuhara Takatoriyama, Japan	TeNLE	*Abies firma*
45	Pasoh, West Malaysia	TrBLE	Dipterocarpaceae, Fagaceae, Burseraceae, Leguminosae, Euphorbiaceae, Myrtaceae
46	Meerdink, Netherlands	TeBLD	*Quercus petraea, Fagus sylvatica, Sorbus aucuparia, Frangula alnus*
47	Geobotanical Station, Bialowieza, Poland	TeBLD	*Carpinus betulus, Tilia cordata, Picea excelsa, Acer platanoides, Quercus robur, Ulmus campestris, Fraxinus excelsior*
48	Ispina, Niepolomice near Krakow, Poland	TeBLD	*Quercus robur, Carpinus betulus, Tilia cordata*
49	Kampinos National Park, Poland	TeNLE	*Pinus sylvestris, Quercus robur, Betula verrucosa*
50	Babadag, Site 1, Rumania	TeBLD	*Quercus pubescens*
51	Babadag, Site 2, Rumania	TeBLD	*Quercus pedunculiflora, Acer tataricum*
52–53	Sinaia, Site 1, Rumania	TeBLD	*Fagus sylvatica, Abies alba*
54	San Juan, Spain	TeNLE	*Pinus sylvestris*
55	Andersby Angsbackar III, Sweden	TeBLD	*Quercus robur, Betula pubescens, Betula verrucosa*
56	Kongalund Beech Site, Sweden	TeBLD	*Fagus sylvatica*
57	Kongalund Spruce Site, Sweden	BoNLE/P	*Picea abies*
58	Langarod, Sweden	TeBLD	*Fagus sylvatica*
59	Linnebjer, Sweden	TeBLD	*Quercus robur, Tilia cordata, Sorbus aucuparia, Corylus avellana*
60	Oved, Sweden	TeBLD	*Fagus sylvatica*
61	Koinas, Arkangelsk Region, USSR	BoNLE	*Picea abies*

(*Table* 1.1 *continued*)

Site no.	Name	Forest type	Principal overstory components
62–63	Caucasus Birch, Azerbaijan, USSR	TeBLD	*Betula pendula*
64–67	Tallish Ironwood, Azerbaijan, USSR	TeBLD	*Parrotia persica*
68–69	Tallish Oak, Azerbaijan, USSR	TeBLD	*Quercus castaneifolia, Zelkova carpinifolia, Parrotia persica*
70–71	Les Na Vorskl, Plot 7, Belgorod Region, USSR	TeBLD	*Quercus robur, Tilia cordata, Acer platanoides, Ulmus scabra*
72	Central Forest Reserve, USSR	BoNLE	*Picea abies*
73–89	Southern Karelian Spruce, Karelia, USSR	BoNLE	*Picea abies*
90	Tigrovaya Floodplain, Tadjikistan, USSR	TeBLD	*Populus prunosa, Elaeagnus angustifolia*
91	Meathop Wood, United Kingdom	TeBLD	*Quercus petraea, Quercus robur, Betula pendula, Betula pubescens, Fraxinus excelsior, Corylus avellana*
92–94	Black Spruce, Alaska, USA	BoNLE	*Picea mariana*
95	Hubbard Brook, New Hampshire, USA	TeBLD	*Acer saccharum, Betula lutea, Fagus grandifolia*
96	Brookhaven, New York, USA	TeBLD	*Quercus alba, Quercus coccinea, Pinus rigida*
97	Watershed 1, Coweeta, North Carolina, USA	TeNLE/P	*Pinus strobus*
98	Watershed 18, Coweeta, North Carolina, USA	TeBLD	*Acer rubrum, Quercus prinus*
99	Duke Forest, North Carolina, USA	TeNLE/P	*Pinus taeda*
100	Saxapahaw, North Carolina, USA	TeNLE/P	*Pinus taeda*
101	Andrews Experimental Forest, Watershed 10, Oregon, USA	TeNLE	*Pseudotsuga menziesii, Tsuga heterophylla, Castanopsis chrysophylla, Thuja plicata, Pinus lambertiana, Acer macrophyllum*
102	Liriodendron Site, Oak Ridge, Tennessee, USA	TeBLD	*Liriodendron tulipifera, Quercus spp., Carya tomentosa, Pinus echinata*
103–106	Walker Branch, Oak Ridge, Tennessee, USA	TeBLD	*Quercus alba, Quercus prinus, Quercus velutina, Pinus echinata, Liriodendron tulipifera*
107	Thompson Research Center, Seattle, Washington, USA	TeNLE/P	*Pseudotsuga menziesii, Tsuga heterophylla*
108	Noe Woods (Lake Wingra), Wisconsin, USA	TeBLD	*Quercus alba, Quercus velutina, Prunus serotina*
109	Nakoma Urban Forest, Wisconsin, USA	TeBLD	*Quercus alba, Quercus velutina*

(*Table* 1.1 *continued*)

Site no.	Name	Forest type	Principal overstory components
110	Fa. Eglharting, Abt. 27A, Federal Republic of Germany	BoNLE/P	*Picea abies*
111–113	Solling Project, Federal Republic of Germany	TeBLD	*Fagus sylvatica*
114–116	Solling Project, Federal Republic of Germany	BoNLE	*Picea abies*
117	Lubumbashi, Zaire	TrBLD	*Marquesia macroura*

included environmental (climatic) zonation or management status. The Holdridge system (Holdridge, 1964) was also consulted, and a degree of gross bioclimatic categorization was incorporated in the final classification.

A hierarchical scheme was used, ultimately consisting of four major units – climate, life-form, behavior, and status. The last three are dichotomous, while four divisions of the climatic regime were necessary to encompass all woodland sites. Twenty-six research sites were classed as *Tropical*, three as *Mediterranean*, 55 as *Temperate*, and 33 as *Boreal*. With respect to life-form, 72 sites were dominated by broad-leaved species, while 45 were needle-leaved. Behavior was more evenly divided; 65 stands are deciduous, and 52 evergreen. Finally, 89 sites consist of natural forest, while 28 are managed plantations. There is a reasonable representation of all categories with the exception of Mediterranean woodlands, where a paucity of sites relates, at least in part, to the small number of contributing nations with Mediterranean climate.

All 117 sites, categorized according to the derived classification, are listed in Table 1.1. This array correlates with the Woodlands Data Set (DeAngelis, Gardner & Shugart, Chapter 11), and the nomenclature is used in the other chapters as well.

Mediterranean woodlands

Three sites are available that are representative of woodlands in Mediterranean climates, one in Australia and two in southern France. Characterized by warm, dry summers and cool moist winters (Emberger *et al.*, 1963), the vegetation of these regions is unique, consisting for the most part of sclerophyllous trees and shrubs with an understory of herbs and grasses (di Castri & Mooney, 1973) (Fig. 1.2).

In Australia, the IBP site is located in the Mt Disappointment State Forest in southern Victoria. It is dominated exclusively by messmate or messmate stringy bark (*Eucalyptus obliqua*) (Rule, 1967) that forms a

continuous overstory approaching 30 m in height. The stand is somewhat over 50 years old, formed on a Krasnozem (a red, friable, porous soil) overlying metamorphosed mudstones, sandstones, and shales of Silurian age. The soils are well drained and acid, with pH ranging from about 5.2 to 5.9. Mean annual precipitation is 962 mm. The region is frost-free, with a mean annual temperature of 11°C.

The understory is relatively sparse, consisting primarily of shrubs (*Xanthorrhoea australis*, *Adenanthos terminalis*, *Acacia* spp., *Hakea* spp.) from 0.5 to 2 m tall, perennial grasses (*Themeda australis*, *Stipa pubescens*), and an admixture of herbs (*Lepidosperma canescens*, *Lomandra dura*, *Kennedia prostrata*). Recently published documents do not yield much additional information on species composition, although Adamson & Osborn (1924), Lawrence (1939), and Specht (1972–3) are useful references. The site has a basal area of 58.7 m^2/ha, at densities ranging from 705 to 946 trees per hectare. The leaf area index is 4.1, and above-ground standing crop is 31.2 kg/m^2.

The two sites in southern France straddle the city of Montpellier, home of one of the world's great schools of phytosociology. The site at Madeleine lies at 10 m, while Rouquet is at 180 m above mean sea level. Both sites are dominated by holly-leaf oak (*Quercus ilex*), reaching heights of 11 m at Rouquet and 15 m at Madeleine. Rouquet has been coppiced, and the present stand age is about 150 yr. Based on height, Madeleine appears older, although supporting data on age are not available. Additional height may be a function of density, as Madeleine has a density of only 527 trees per hectare, while Rouquet displays 1440 trees per hectare. Herbaceous understory is poorly developed at Rouquet, while that at Madeleine is 90%

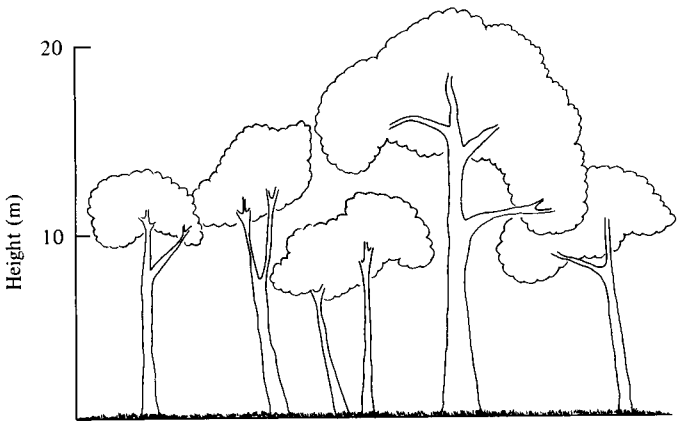

Fig. 1.2. Profile diagram of Medterranean Woodland, southeastern Australia. Overstory of *Eucalyptus obliqua*.

Hedera helix (English ivy) (Lossaint, 1973). Other species typically present are *Ruscus aculeatus*, *Rosa sempervirens*, *Vinca major*, and *Asparagus acutifolius*. All of these, like the overstory, are both sclerophyllous and evergreen.

These sites are also frost-free, with mean annual temperatures of 14.1 and 13.4°C. Precipitation is 754 mm at Madeleine, but rises to 987 mm at the higher elevation at Rouquet. Both sites are on dolomitic limestone, with slightly basic, rendzina-type soils. Drainage is good, with the soils containing 8 to 9% organic matter.

In disturbed areas, *Quercus ilex* is replaced by *Q. coccifera*, a shrubby, sclerophyllous scrub oak that dominates the 'garrigue' of the Mediterranean coast (Reed, 1954). Grazing pressure then creates, through time, a grassy pasture composed predominantly of *Brachypodium ramosum*.

The Mediterranean woodlands are not, of course, extensive on a global scale, as most of the native communities are dominated by shrubs. The small representation of the sites does, however, give a reasonable characterization of the type, and a range of both environmental characteristics and phytosociological parameters.

Tropical forests

The tropical forests represented in the IBP Woodlands Data Set are represented by 26 sites, 18 of which are managed plantations at two locations in northeastern India. The remaining eight sites are evenly divided between true rain forest and broad-leaved deciduous forests on the subtropical fringe. The three great regions of tropical rain forest are represented (Aubert de la Rüe, Bourlière & Harroy, 1957), by a neotropical site in Brazil (Manaus) (Fig. 1.3), two in Africa (the Ivory Coast), and one in western Malaysia at Pasoh.

The latitudinal span is about 40°, from 11° 29′ S in Zaire to 27° N at the Indian sites at Gorakhpur. This gradient is somewhat misleading, however,

Fig. 1.3. Profile diagram of tropical deciduous forest near Manaus, Brazil. Modified from Huetz de Lemps, 1970.

as all but Lubumbashi, Zaire, lie in the northern hemisphere. Among the rain-forest sites, annual precipitation ranges from 1739 mm at Yapo in the Ivory Coast to 2095 mm nearby at Banco. All four sites are lowland, ranging to only 100 m above mean sea level at Pasoh. Mean annual temperature is 26–7°C.

Four deciduous sites, three at Chakia in India and one in Zaire, illustrate a dry season dormancy. Consequently, the growing seasons are 270 days (nine months) at Chakia, but only 118 days (four months) at Lubumbashi. The latter lies at an elevation of 1208 m, while Chakia is only 350 m above mean sea level. Precipitation at Chakia is 844 mm, with a mean annual temperature of 30°C. Comparable values for Lubumbashi are 1273 mm and 20.3°C, respectively. Thus, the site in Zaire receives half again as much rain as Chakia, in roughly half the length of time. The effects of the monsoons that sweep north off the Bay of Bengal are evident particularly when compared to the decidedly continental climate in the interior Congo basin.

The 18 Indian broad-leaved plantations lie at 81 m, with a mean annual temperature of 27.5°C and a rainfall of 1158 mm. These plantations, six each of teak, sal, and mixed teak and sal, differ only in age. No data are available on soils or underlying geology.

Soils in the eight natural forests of this series (the four rain-forest and four deciduous sites) are pale yellow to reddish latosols, formed mostly on ancient igneous or metamorphic rock. Drainage is medium to rather poor. The rain-forest soils are strongly acid, with pH ranging from 3.1 to 5.1, while those of the deciduous sites are less so, with values from 5.0 to 6.8.

Tropical rain forest

Tropical rain forest, the epitome of forest everywhere, is a highly productive and diverse formation — one that has been both an inspiration and an enigma to plant geographers and ecologists since the days of Alexander von Humboldt. The forest is well stratified, often with five well-defined layers, including emergent, canopy, sub-canopy, shrub, and herbaceous synusiae (Richards, 1952; Fig. 1.4). Among the tree species, dominance, as it is commonly recognized in temperate forests, has little relevance; the most abundant species may be present at densities of no more than two or three per hectare. Therefore, it is often the practice to discuss dominance in terms of plant families, where several genera may collectively assume a position of importance in the community (Meggers, Ayensu & Duckworth, 1973). Among the four IBP sites, this practice has been followed, although specific information is available for major species at the two sites in the Ivory Coast. The dominants come either from tropical families (Palmae, Olacaceae) or from large, cosmopolitan ones (Leguminosae, Rosaceae), as is apparent in Table 1.2. Note that species of Burseraceae and Leguminosae

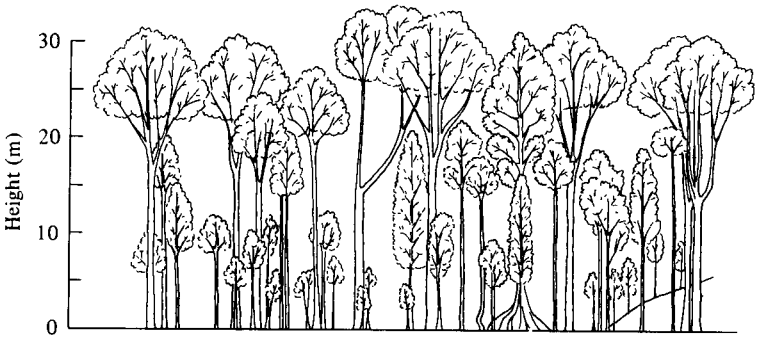

Fig. 1.4. Profile diagram of tropical rain forest showing layers (synusiae) of woody components. Modified from Richards (1952).

are dominant at all four sites. The former is a tropical family of 16 genera and approximately 500 species, all trees or shrubs. Major genera are *Protium*, *Commiphora*, *Boswellia*, *Bursera*, *Canarium*, and *Santiria*. Conversely, the legumes are the third largest family of flowering plants, with about 600 genera and over 12 000 species. There is a heavy concentration of legumes in the tropical regions, particularly in the Amazon Basin of South America.

The forest at Manaus is mature, 38 m tall, with a standing crop of 40.6 kg/m^2. Basal area is 30.7 m^2/ha, but the stocking density is questionable. Tree density probably approaches 1000 per hectare. The mature forests at Banco and Yapo are physiognomically similar, with basal areas of 30 and 31 m^2/ha, and standing crops of 51 and 45 kg/m^2, respectively. Reported densities are 265 trees/ha at Banco and 427 trees/ha at Yapo.

The Ivory Coast sites share the dominants *Allenblackia floribunda* (Guttiferae), *Coula edulis* and *Strombosia glaucescens* (Olacaceae), and *Dacyrodes klaineana* (Burseraceae). In addition, *Turreanthus africana*, the leguminous *Berlinia confusa*, *Combretodendron africanum*, and *Chrysophyllum* sp. are present at Banco. Yapo includes *Scottelia chevalieri*, *Scytopetalum thieghemii*, *Tarrietia utilis*, and the legume, *Piptadeniastrum africanum*. Neither subcanopy nor understory species lists are available for either site, but Aubréville (1938) (reproduced in Richards 1952, *p.* 51) gives a list of 74 species (both over- and understories) in the forest at Massa Me, Ivory Coast. His list includes *Piptadeniastrum*, *Combretodendron*, *Strombosia*, *Scottellia*, *Allanblackia*, *Coula*, etc., so species composition is similar to the forests at Banco and Yapo. In addition to reproduction of the dominant tree species, the understory includes representatives of *Cola* (two species), *Diospyros* (two species), *Baphia* (two species), *Albizzia* (legumes), *Hannoa*, *Myrianthus*, and *Napoleona*.

The site at Pasoh, Malaysia (Fig. 1.5), is dominated by dipterocarps