

### **Lime-trees and Basswoods**

A Biological Monograph of the Genus *Tilia*

Lime-trees (*Tilia* spp.) are widely distributed and locally important members of northern temperate broad-leaved forests. In marked contrast to the largely uniform morphology of the genus, described in the first two chapters, its taxonomic treatment has become increasingly confused and controversial, with over 100 species described.

Using extensive data from field studies of natural populations throughout the native distribution, this book clarifies the situation, proposing a revised taxonomy of 23 species and 14 subspecies. Detailed descriptions are provided for all recognised taxa and are accompanied by illustrations. Data from herbaria and cultivated trees are used to extend the analyses where appropriate and type specimens are included to ensure stable nomenclature. The distribution and general ecology is summarised for each species.

The final chapters are devoted to the geological history of the genus, the physiological and reproductive ecology of the most fully studied species and the association of lime-trees with human culture, including their utilisation and cultivation.

DONALD PIGOTT is a past director of the Cambridge University Botanic Garden and former Professor of Biology and Head of Department at the University of Lancaster. He has spent over 15 years extending his earlier studies of the genus *Tilia* to cover its full natural range from Japan and China, to Europe, eastern North America and Mexico.

Donald Pigott

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A Biological Monograph of  
the Genus *Tilia*



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**To Margaret, Julia and Sheila**

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## Preface and acknowledgements

Lime-tree, basswood, duan, Linde, lípa, shinanoki, tilleul and many more: there are as many names as there are languages in the regions where this very distinctive tree is native, for it is surely one of the most easily recognised trees of the woods of the northern temperate zone and, until the advent of the car, one of the most loved and respected. Ever since Carl Linnaeus accepted the classical name *Tilia* for the genus, there has never been any confusion about its identity.

The same cannot be said of the species, however, of which the names, and the trees to which they refer, began with a confusion and have continued in much the same way up to the present day. Linnaeus himself was very familiar with the native lime-tree of southern Sweden that was, and still is, common in woods and meadows around his family home. It was also the tree from which his family had taken its name. Unfortunately, he did not distinguish it from the large tree that still grows at Uppsala University, from which he probably took the one specimen that he labelled *T. europaea*, and which remains in his herbarium in London. Thus the name that he surely intended for the widespread species for which we now use Miller's name, *T. cordata*, is, by the rules of nomenclature, applied to the hybrid of that species with *T. platyphyllos*. Even Miller's name, *T. cordata*, proves not to have priority, but it is so well established that a proposal to conserve it has been accepted. Indeed, a simple measure of the general confusion is that more than 200 names of species of *Tilia* have been published for what, in my opinion, is about a tenth of that number of species.

Before embarking on this project, I had discovered, as evidently Linnaeus had before me, that even with only two native species in Britain, and with both natural and planted hybrids between them, correct identification is not learnt easily or quickly. The reasons for this are discussed in later chapters but essentially the solution is to study whole trees, collect flowering or fruiting specimens for taxonomic purposes and, if possible, first study natural populations. To extend

this discipline over the whole native range of the genus has only been possible with generous financial grants and with co-operation and help from a very large number of people.

A long list of people's names has little to commend it, so I have placed them in their historical and geographical context, and start at the beginning. My lifelong fascination with plants, not just discovering their names but also how they work, stems directly from my mother, Helen Constance Pigott (née Lee), who encouraged me to grow plants, raise them from seeds and learn their names. A large tree grew in our rather marshy garden and, at an early age, I was with her on a visit to Kew Gardens (the Royal Botanic Gardens) when she identified it as *Acer negundo*, box elder (scarcely a recommendation for using English names). I thank her for sowing a seed that grew into my deep interest in trees and a delight in Kew.

As a boy, I had the good fortune to meet, by chance, Mr A.B. Jackson, whom I visited at Kew several times and accompanied on excursions. Then, as an undergraduate, I was taught by Dr H. Gilbert-Carter and took to heart his advice 'when entering a wood, first look up at what is above you' and I fell under the spell of Dr A.S. Watt. From Cambridge, using Babington's *Flora* (1860), I visited the White Wood at Gamlingay and there encountered *T. cordata* with *Convallaria majalis* (lily-of-the-valley), both species that I had not previously seen in the wild, and in a combination that later proved to be significant.

In 1951, I moved to the University of Sheffield and began research on the influence of climate and soils on the vegetation of the Derbyshire upland. While exploring the extensive woods in the limestone dales, in which ash (*Fraxinus excelsior*) predominates in the canopy and was regarded by Moss (1913) and Tansley (1939 pp. 427–8) as the 'natural climax dominant', I came across small populations of lime-trees, usually on cliffs, or steep, rocky outcrops. They invariably consisted of large and evidently old trees of *T. platyphyllos*, rarely *T. cordata*, and often hybrids between them, with no regeneration from seedlings. A field-layer of several unusual species, including *Convallaria majalis*, characterised the sites.

Further investigation provided evidence that these were probably relics of a much older woodland, largely destroyed by clearance and grazing, and then replaced by secondary woodland of ash. In that case, *T. platyphyllos* was surely native, even though the then current *Flora of the British Isles* (Clapham, Tutin and Warburg 1952) treated the species as doubtfully so. The absence of suitable deposits of peat or sediments nearby prevented the use of pollen analysis to confirm these hypotheses. I am much indebted to Professor A.R. Clapham for his support and keen interest in all my work throughout that period.

A brief spell in Cambridge and my move in 1964 to the then new University of Lancaster gave me the opportunity to investigate the causes of failure of regeneration, as it brought me within easy working distance of localities of *T. cordata*, both close to, and at, the north-western limit of its natural distribution. A preliminary study found that these populations, like those in Derbyshire, consisted of large, often very large, old trees with no apparent regeneration from seedlings. Large samples of fruits from several trees at Aughton near Lancaster proved each year to be almost completely sterile, and smaller samples from other sites in the Lake District were the same. A research project was designed to investigate the causes and I thank the Natural Environment Research Council for a sequence of grants to fund this work. I also thank both Mr J.S.R. Chard of the Forestry Commission for proposing that part of this work should be at Grizedale, and members of the staff there for their help. I am indebted to Mrs J.P. Huntley (née Paice) for her enthusiasm and wide range of skills as my research assistant, Mr W.A. Wood, my very able research technician, and Mr W. Blackledge, glass-house technician at Lancaster. Grants from NERC also supported me and Professor W.J. Davies in a joint project on shade tolerance and water relations of young plants of *T. cordata*, and me and my first wife, Margaret Pigott (née Beatson), in palynological studies at Cunswick Tarn, close to localities of *T. cordata* and *T. platyphyllos* (the latter now known to have been planted).

An opportunity to investigate regeneration of *T. cordata* in Poland arose in 1973, when Professor M.J. Dąbrowski suggested that I visit Białowieża. I thank the Royal Society and the Polish Academy of Sciences for financial help, Professor Dąbrowski for making the arrangements, and Ewa Kaminska for her assistance with fieldwork. The results were the stimulus for studies of regeneration in southern England and France, for which I thank the National Trust for permission to set up enclosures on their properties and Mr P.G. Collis and Dr J.P. Sankey for looking after the plots. In France, I thank the Université de Paris 12 and Professor C. Jacquiot for permission to work at the laboratory at Fontainebleau, and the forest officers, first M. J. Gallon and then M. P. Pouvesle, for protecting my plots at the Forêt de Villefermoy for a period of 34 years.

A visit to the Institute at Vácrátót in Hungary, arranged by the Royal Society and Hungarian Academy of Sciences, led to my association with Professor Fekete G., who took me on excursions to study *Tilia* and has since helped me in so many ways. I also thank Dr Géza K. of the Institute for his help with establishing a neotype of *T. tomentosa*.

The mechanism by which climate-controlled seed production in *T. cordata* that Jacqueline Huntley and I had discovered, attracted the attention of Professor D.M. Gates and, in 1978, I was invited to Ann Arbor University in Michigan. From this, a programme to study the ecology and taxonomy of *Tilia* in eastern America evolved, and I thank the Royal Society, the Waldorf Astor Foundation, the University of Cambridge and the Arnold Arboretum of Harvard University for generous financial assistance that over many years enabled me to make field collections in 14 states and work at Harvard. I thank Dr E.W. Wood for enabling me to work in the Harvard Herbaria and Ms G. Wade for help in the library. I thank Dr R.E. Cook for inviting me to work in the Arnold Arboretum and Ms S. Kelley, Ms S. Hardy Brown and Mr K.D. Port for their assistance and Jianhua Li for our co-operative project on the analysis of the DNA of diploid species of *Tilia*. During fieldwork in America, so many people have helped in various ways, but I am especially grateful to Mr A.K. Gholson (Florida, Georgia), Mr C. Ludwig (Virginia), Professor R.K. Peet (Carolinas) and Mr A.E. Radford (Carolinas), who arranged programmes and contacts, and accompanied me, or my wife and me, on fieldwork. I thank Dr G. Williams-Linera of the Instituto de Ecología at Jalapa for arranging a visit to the Sierra Madra Orientale in Mexico and Mr N.P. Pavón for his guidance in the field.

During a visit to the Soviet Union in 1983, which was primarily for the ecological study of deciduous, broad-leaved woodlands, under an arrangement between the Royal Society and Soviet Academy of Sciences for academic exchange, I was also able to visit the Main Botanic Garden in Moscow and the garden of the Ukrainian Academy of Sciences in Kiev. In both gardens, I was permitted to collect herbarium material of several species of *Tilia* from the Caucasus, the far east of Siberia and north China. I became aware, as I had in America, that there seemed to be very real problems in the taxonomic treatment of the genus. I thank Dr N.A. Kokhno and the staff of the gardens for their help and particularly Dr A. Kurdyuk, who subsequently sent me seed samples and literature.

In 1984, I moved to the University Botanic Garden in Cambridge and decided to consolidate and extend my interest in *Tilia* to the whole genus. So, I began to build up a collection to determine chromosome numbers and, I hoped, eventually for molecular analyses. For the next 10 years, Mrs J. Free was my research technician, and I thank her for the wide variety of laboratory work she undertook and especially for her skill in preparation of root-tip squashes and making most of the chromosome counts. I also thank Mr P. Kerley for his care of and

contribution to the living collection, and with Mr N. Willis for their help on collecting expeditions to the Caucasus and America. During this period and the years immediately after, my wife, Sheila Pigott (née Megaw), and I made a series of expeditions, primarily to collect herbarium material and, where possible, seed or scion wood of almost all the species of *Tilia* now accepted.

For several of these expeditions, I received financial assistance from the Royal Society and from corresponding academies, which included the Soviet and subsequently Russian Academy of Sciences, Chinese Academy of Sciences (Academia Sinica), China Association of Science and Technology, British Council, Japan, the Stanley Smith Horticultural Trust, and the University of Cambridge Travel Fund. For all this generous support I express my sincere gratitude.

Two expeditions were made to the Great and Little Caucasus and I thank Professor Dr M.A. Gogolishvili for inviting us to be based at the Central Botanic Gardens in Tbilisi in 1988, Miss M. Bestaeva, our interpreter, and Professor Dr N.G. Tarassashvili, both for his guidance in the field then, and for his and Mrs L. Tarassashvili's hospitality on a second expedition in 1990. A visit to the Crimea in 1992, specifically to study *T. dasystyla*, was arranged through the Botanical Society of the Russian Republic and we thank Dr V. Schatko and Miss I. Volkovskaya for their company and help throughout, and Dr V.N. Golubev for guiding us in the hills near Yalta.

In the summer of 1993, 10 weeks were spent in China visiting sites in Hebei, Sichuan, Yunnan and Guangdong. Two more visits of two to three weeks' duration were made to Sichuan and Hubei in 1995, and to Jiangxi in 1996. Studies of herbarium material, especially types, were made in Beijing, Chengdu, Guangzhou, Kunming, Lushan (Botanic Garden) and Nanchang (Agricultural University), and I thank the staff of all these herbaria for their help and for providing translation. From each city, several expeditions were arranged and I express my sincere thanks to those who accompanied us in the field, shared their expert knowledge with us and helped us in every way. I also thank our drivers and the many local people who guided us and acted as tree-climbers for collecting specimens. From so many, I must, however, select for special thanks Professor Fu De-zhi (Xiangshan, Beijing), Professor Hu Chi-ming (Guangzhou), Professor Lai Shu-shen (Lushan), Dr Liu Ni-an (Guangzhou), Professor Qin Hai-ning (Xiangshan, Beijing), Professor Ren Xian-wei (Beijing), Mr Tan Ce-ming (Jiujiang Forestry Institute), Dr Yang Guang-yao (Nanchang), Professor Yin Kai-pu (Chengdu), Professor Yu Zhi-xiong (Nanchang) and Professor Zhang Zhi-ming (Beijing).



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During my early studies of *Tilia*, mainly in Britain and Europe, I worked with my first wife, Margaret, and, on fieldwork, I was accompanied by our daughter, Julia, and I thank them for their interest, contribution and support. Since 1985, I have travelled extensively for fieldwork in Europe, Asia and North America, and my wife, Sheila, has been my constant companion and field assistant, often in wild and remote places. She has also helped me and supported me during the years of writing and preparing this monograph, finally checking and correcting the whole text, for all of which I thank her sincerely.