# Tilia L. – Lime

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PRESENT DISTRIBUTION IN THE WESTERN CARPATHIANS

*Tilia cordata* is a characteristic species of mesophilous mixed species deciduous forests found in moderately fertile and fertile habitats of the lowlands and foothill zone (Carpiniom betuli alliance). The taxon is a component of the Tilio-Carpinetum and Potentillo alba-Quercetum associations. In the Carpathians, Tilio-Carpinetum, the oaklime-hornbeam forest, extends i.a. in the submontane belt up to ca 550-600 m a.s.l. (Matuszkiewicz W. 2002). Apart from lime, it includes Fagus sylvatica, Quercus (Q. robur, Q. pubescens, Q. petraea), and Acer (A. pseudoplatanus, A. platanoides, and A. campestre), depending on ecological and geographical conditions. Lime is also frequently accompanied by Carpinus betulus, Picea abies, Abies alba and Pinus sylvestris (Jaworski et al. 2005, Radoglou et al. 2008). Lime stands dominated by T. cordata are more commonly found in Eastern Europe (Radoglou et al. 2008). In the Polish Carpathians they are infrequent. However one example, amongst others, is the "Obrożyska lime forest" nature reserve which is considered to be a relict of the lime forests that developed during the Holocene climatic optimum (Środoń 1991). Tilia platyphyllos is found within beech forests, sycamore forests and lime-sycamore forests (Tilio platyphyllis-Acerion pseudoplatani), that occur across the entire Polish Carpathians (Matuszkiewicz W. 2002, Radoglou et al. 2008).

## Ecology

Four lime species are native to areas of Europe: *Tilia tomentosa* (Moench.), *Tilia dasystylia* (Stev.), *Tilia cordata* (Mill.), and *Tilia platyphyllos* (Scop.). However only the two last-mentioned are found in Poland. *T. platyphyllos* attains its NE limit of occurrence in that country and grows exclusively in its southern part, up to latitude 52°N (Boratyńska & Dolatowski 1991, Zając & Zając 2001). The growth of lime is determined mainly by temperature. *T. cordata* requires a mean annual temperature of +2°C and mean July temperature of +17°C (Boratyńska & Dolatowski 1991, Pigott & Huntley 1980). It is nearly certain that the southern range of occurrence of the species is limited by periods of summer droughts affecting the Mediterranean region. *Tilia platyphyllos* inhabits lowlands and foothills of montane regions in Central and Southern Europe. In the Alps it attains altitudes up to 1800 m a.s.l. (Boratyńska & Dolatowski 1991). It is less resistant to low temperatures, drought and dry winds than *T. cordata*. In less favourable conditions, particularly in areas close to the limit of its range, lime is able to develop a shrub form (Radoglou et al. 2008). *Tilia* species are mesocratic and lose out in competition with trees more tolerant of shading, such as *Abies, Fagus, Carpinus*, and *Picea*.

Limes are known to prefer fresh or moderately humid soils with mull or moder humus. They also grow in areas with higher amounts of calcium in the soil (Jaworski 1995, Radoglou et al. 2008). *T. cordata* may be found in habitats with a shallow water table and is generally tolerant of shading (Pigott 1991). It is highly capable of vegetative reproduction and develops offshoots from cut and fallen stems (Pigott 1989). The high rate of decomposition of its leaves is likely to positively affect the development of forests on poor soils (Radoglou et al. 2008).

All lime species are anemochores. Diaspores are dispersed by wind action, using a long bract integrated with the infructescence and functioning as a wing (Lang 2003). Flowers and seeds are first formed after ca 10-30 years of growth, earlier in trees developed from offshoots. Seeds are produced each year. Most of them fall to the ground in autumn, however some remain on the trees and drop down with snow, which is of a great ecological importance as from the snow surface seeds are dispersed at greater distances by the wind (Radoglou et al. 2008). Young limes grow slowly and attain a height of ca 3.5 m. Following Faliński and Pawlaczyk and their studies in the Białowieża Primeval Forest, the continued presence of lime in tree stands results from its great vitality and flexibility in adaptations to changing ecological conditions (Faliński & Pawlaczyk 1991).

## EXPANSION IN EUROPE DURING THE LATE GLACIAL

During the maximum cooling of the Late Glacial part of the Vistulian glaciation, *Tilia* inhabited areas of the Balkan Peninsula (e.g. Willis & Niklas 2004, Tzedakis et al. 2002), the Apennine Peninsula and the southern and southeastern peripheries of the Alps (e.g. Allen et al. 2000, Bennett et al. 1991, Lang 2003, and Kaltenrieder et al. 2009, including other references). Palynological data from the Bulgarian mountains, the Rila Mountains (Božilova 1995), and the southern foothills of the Carpathians (Farcas et al. 1999) suggest that in advantageous microclimatic conditions lime is likely to have survived the glacial period also in small areas of these regions. Studies by Jankovská and Pokorny (2008) indicate that lime may have also survived in isolated pockets within the area of Slovakia (e.g. in the Southern Slovakian Karst). At present, there are no solid grounds for considering the Iberian Peninsula, North-East Russia, western Siberia or the coast of the Black Sea as refugial areas of European limes (Lang 2003).

At the beginning of the present interglacial, *Tilia* migrated from the Alps and the Carpathians into Western and North-Western Europe. At ca 9000 BP the taxon was already found in South Poland (Kupryjanowicz et al. 2004) and between 5000 and 4000 BP (7000 and 6000 cal. BP) it attained, and even most likely crossed, its present-day northern limit of occurrence (formed by *T. cordata*) in Europe. The rate of lime migration varied between regions. According to Lang, during the Boreal period Central Europe was marked by a rapid (ca 820–670 m/year) northwards migration of *Tilia* (Lang 2003).

This stage of immigration was followed by phases of expansion in abundance and establishment of populations. Estimation of the duration of time separating the two phases differs greatly at particular sites and ranges from ca 400 to 2500 years (average 1000 years). During this time, lime successfully competed with other trees occupying these areas (Lang 2003). In Poland expansion of lime was observed from ca 9000/8500 to 6500 BP. The taxon attained its maximum distribution during the Atlantic period of the Holocene, at ca 6000 BP (Kupryjanowicz et al. 2004), and sensitised, as at present, of two species: T. cordata and T. platyphyllos. Although their pollen grains show distinct differences in most pollen profiles they were not determined to the rank of species, therefore it was not possible to investigate the Holocene history independently for both taxa (Christensen & Blackmore 1988). Huntley and Birks (1983) interpreted the frequency of 1% as the minimum value indicating the local occurrence of single trees of lime, 5-10% – as evidence of its high proportions in forests, and amounts exceeding 10% – as record of its local dominance in tree stands.

Decrease in the amounts of *Tilia* most likely resulted from many factors, comprising climatic changes and, undoubtedly, intensified human activity. Grant et al., in their analysis of reasons for the Holocene decrease in proportions of lime in Great Britain, state that ca 44% of such changes depend on processes other than human pressures (Grant et al. 2011). European isopollen maps illustrate a southwards withdrawal of *Tilia* from its northern limit of occurrence (Huntley & Birks 1983). For the period from ca 3750 BP (5700 cal. BP) this process is explained by the deteriorating climatic conditions, while for the time since ca 1250 BP (3200 cal. BP) – mainly by human activity.

HISTORY OF EXPANSION IN THE WESTERN CARPATHIANS DURING THE HOLOCENE (Fig. 23)

#### 10 000-9500 BP

Where pollen diagrams record the first, often single *Tilia* pollen grains, these most likely originated via longdistance transport, i.e. from southern refugial areas.

## 9000 BP

Lime began to migrate into the Polish Carpathians. Its highest amount, 1.1%, exceeding the minimum value indicating the local occurrence of taxon, is recorded in the area of the Jasło-Sanok Depression at the site of Besko. Values of 0.7% lime were attained at Bryjarka (site no. 212), in the western part of the Beskid Sądecki range and in the Tatra Mountains, where pollen was being transported from the south.

#### 8500 BP

According to the outline of isopolls, the range of occurrence of Tilia extended over the entire Carpathians, except for the Tatra and Bieszczady Mountains and the Beskid Sądecki range. Two centres of lime distribution were observed. The taxon expanded into the Jasło-Sanok Depression and was found locally in the areas of Besko - site no. 232, 233 (4.1%) and Jasło - 120 (2.2%). In the Beskid Makowski range, values varied between sites. The amount of 10.7%, recorded near the site of Pcim-Sucha (265), indicates the likely dominance of lime in forests. Tilia was of clearly lower importance in the surroundings of the Bogdanówka-Beło site (277) marked by a pollen frequency of 2.5%. Data from the sites of Bobrov (285), in the Slovakian Upper Orava (with a value of 1.8%), and Puścizna Rękowiańska (111), in the Orawa-Nowy Targ Basin (1.6%), confirm the local, rather occasional, appearance of lime in the lower montane forest zone. The pollen profile from Tarnawa (257) in the Bieszczady Mountains includes a value of 1.8%.

Undoubtedly, *Tilia* arrived in the Carpathians using two migration pathways. The first one, located to the west of the Carpathians, most likely passed through the Moravian Gate (Kupryjanowicz et al. 2004), from where lime spread to the east and south, along the Vistula and Raba river valleys, and proceeded to expand into the Beskid Makowski, Beskid Mały and Beskid Wyspowy ranges which is marked by isopoll of 2% and 5%. The second migration pathway may have included the passes of the Beskid Niski range, from where *Tilia* extended its range into lower altitudes of submontane areas, i.e. into the Jasło-Sanok Depression indicated by an isopoll of 2%.

## 8000 BP

The abundance of *Tilia* rapidly increased in the Jasło-Sanok Depression, where a value of 7.6% was recorded in Besko (233) and 16.6% in Tarnowiec (123). Maximum frequency, 18.3%, were observed in the northern part of the Beskid Niski range, in Szymbark (126), areas of which were most likely covered by stands comprising lime as a co-dominant species. For both areas and for neighbouring parts of Pogórze Ciężkowickie, as well as Pogórze Dynowskie Foothills, the proportion of lime is determined by isopoll of 10%. The Raba river valley remained the second centre marked by higher lime values (9%). The outline of the isopolls shows an intensive broadening of the range of occurrence of the taxon. Its amounts increased to 2.7% near Tarnawa in the Bieszczady Mountains, though Tilia did not inhabit the site itself and was rather found at lower altitudes of submontane areas. During this period, lime was a component of mixed deciduous forests in the entire area of the Polish Carpathians, excluding higher locations of the Tatra and Bieszczady Mountains.

## 7500 BP

It must be taken into account that the outline of isopolls is clearly affected by the low number of sites available for plotting on the maps. Data from dot maps indicate a slight increase in the proportion of lime in stands in the western part of the Carpathians: the Beskid Żywiecki and the Beskid Makowski ranges and the Orawa-Nowy Targ Basin. *Tilia* was still frequently found in communities surrounding the site of Pcim-Sucha (265) in the Beskid Makowski range (pollen value of 9%) and in areas of Szymbark (126) in the Beskid Niski range (8.6%). For both areas the highest values in the Western Carpathians are marked by the 5% isopoll. Low amounts of the taxon, or even its absence, were recorded at higher altitudes of the Beskid Niski range and the Tatra Mountains, indicated by isopolls of 0.5% and 1%.

## 7000-6000 BP

High values, however showing a slight decrease (from ca 11-7%), were recorded in the Raba river valley. A simultaneous increase (from 8.4-10.2%) was observed in the Beskid Makowski range at the site of Bogdanówka-Beło (277). The highest amounts (17.5%) were still recorded in the Jasło-Sanok Depression, which was at least locally, in areas of Tarnowiec (123), occupied by lime-dominated stands. Isopollen maps indicate the abundant occurrence of Tilia in deciduous forests of the Polish and Slovakian part of the Beskid Niski range (Szymbark – 126; ca 6.2%, Regetovká – 61; 4.4%). The Beskid Żywiecki range and the Orawa-Nowy Targ Basin were marked by stable, low frequency of 2-3%. Lime was found occasionally in the Tatra Mountains (Molkówka – 264; ca 2%), however not at higher altitudes. The outline of isopolls plotted for 6000 BP is affected by the lack of palynological data for the Jasło-Sanok Depression. The period is typified by an increase in values of *Tilia* in the Beskid Sądecki range (Jesionowa – site 261; 7.6%). The map illustrates also the repeated separation of centres with high amounts of the taxon marked by the 5% isopoll and the likely decrease in lime frequency in parts of the Beskid Wyspowy range and the Pogórze Ciężkowickie Foothills.

### 5500-4500 BP

A gradual regression of lime begins in Carpathian regions located to the west of the Dunajec river valley. The previous centre of occurrence of this taxon, in areas of the Raba river valley and the Beskid Makowski range, became clearly less important, as shown by pollen values decreasing from ca 7% to 4% and the smaller area indicated by the 5% isopol. Similarly, amounts of Tilia in the Orawa-Nowy Targ Basin decrease from 3.9% to 2.1%. Lime may have occasionally grown in the Tatra Mountains. Its frequency was similar in the Beskid Sądecki range (ca 3%) and at higher altitudes of the Beskid Niski range (Regetovká – 61; 3.9–2.6%, Jasiel – 125, 0.7–1.7%). The Cergowa Góra Mt. (124), with a proportion of 17.3%, indicating an intensive development of lime-dominated forests, is as exception. In the same period, values for Tilia rapidly increase in the Beskid Niski range (Szymbark - 126; 14-10%) and in the Jasło-Sanok Depression (Tarnowiec -123; 10.6%). In this area lime was an important element in the forest, as clearly marked by a widening of the 10% isopoll band on the map for ca 4500 BP.

## 4000 BP

Lime continued its withdrawal from areas located to the west of the Dunajec river. However, single trees remained in the Beskid Żywiecki range, the Tatra Mountains and the Orawa-Nowy Targ Basin. Tilia was slightly more frequent in forests of the Beskid Makowski and Beskid Sądecki ranges and the middle Raba river valley, where the proportion of lime is indicated by the 2% isopoll. Lime pollen values in the Jasło-Sanok Depression were strongly reduced (Tarnowiec - 123; 4.3%; Besko - 232, 233; 2.2%). High proportions were still recorded in areas of Szymbark -126 (11.7%) and Cergowa Góra Mt. - 124 (7.6%) in the Beskid Niski range and most likely typified also the Pogórze Ciężkowickie Foothills. Higher locations of the Beskid Mountains were generally marked by lime values slightly higher than in the preceding period (Regetovká - 61; 3.9%, Jasiel - 125; 2.2%).

## 3500-2000 BP

The importance of lime at recorded sites proceeds to decrease, though unevenly, but more rapidly in areas located to the west of the Dunajec river covered by isopolls of 1% and 2%. High values are no longer recorded in the Pogórze Ciężkowickie Foothills and the Beskid Niski range. The data indicate that in most Western Carpathian areas lime was found in minor amounts, but was slightly more frequent to the east of the Dunajec river. Higher parts of the Tatra and Bieszczady Mountains, the Beskid Żywiecki and Beskid Śląski ranges, and from ca 2500 BP also the Beskid Sądecki range and the Gorce Mountains, are devoid of Tilia. In the Jasło-Sanok Depression the taxon is only infrequently present, with values of ca 1.4–3.3%. More favourable conditions for the growth of lime were still observed to the east of the Dunajec river, particularly in the Beskid Niski range and areas of Szymbark (126) and the Maślana Mountain (280), initially also on the Cergowa Góra Mt. (124). The taxon had gone from the vicinities of Regetovká (61) and Jasiel (125). Local dominance of Tilia in forests, shown by pollen values of 20-14% and occurrence of its macrofossil remains in sediment (Wacnik, unpubl.), was recorded exclusively in Kružlová (62), in the Slovakian part of the Beskid Niski range, for ca 3000–2500 BP. However, even here the amounts of lime decreased, to 4.1% by ca 2000 BP. Results from this site strongly affect the outline of isopolls indicating high Tilia values in the borderland of the Beskid Mountains. Almost the whole area located to the east from the Dunajec river is covered by isopolls of 2% and 5%.

## 1500 BP

During this period, lime was found in minor amounts in forests of the eastern part of the Carpathians, excluding the Bieszczady Mountains. To the west of the Dunajec river it occurred only locally in the Beskid Żywiecki range, middle Raba river valley and in the adjacent areas of the Beskid Makowski and Beskid Wyspowy ranges (covered by isopoll of 1% and 2%). The only exception was the site in the Maślana Góra Mt. (280) area with value of 7.6%.

## 1000-500 BP

According to the maps, *Tilia* survived only locally in the Beskid Niski and Beskid Żywiecki ranges and in the Pogórze Dynowskie and Ciężkowickie Foothills. It is shown by the 1% isopoll.

### 0 BP

Palynological data, providing a basis for plotting an isopollen map, are insufficient and limited to the borderland. They do, however confirm the presence of lime in areas of the Beskid Żywiecki, Beskid Śląski and Beskid Mały ranges. Undoubtedly, this fragmentary record may be completed with the use of maps of the present-day distribution of *Tilia* in the Carpathians which indicate occurrence of the taxon in the entire study area (Zając & Zając 2001).

#### CONCLUSIONS

Lime migrated into the Polish Carpathians ca 9000 BP from glacial refugia located in Southern Europe. It may be assumed that refugia of the Slovakian Carpathians greatly contributed to this process. Two migration pathways of Tilia were distinguished: the Moravian Gate and passes of the Beskid Niski range. First limes arrived most likely in the area of the Jasło-Sanok Depression. Ca 8500 BP they rapidly expanded and formed two centres of occurrence, located in the above-mentioned Depression and in the region of the middle Raba river valley. Already at ca 8000 BP the Jasło-Sanok Depression and the adjacent parts of the Beskid Niski range were occupied by limedominated forest communities. Tilia was also an important forest-forming component in the middle Raba river valley. Since ca 7000 BP the taxon developed intensively in the Beskid Makowski range and attained its maximum proportions in Carpathian stands. Only the highest areas of the Tatra and Bieszczady Mountains were beyond its range. An important stage in the Holocene history of the genus dates to 5500-4500 BP, when the first signs of a gradual withdrawal of lime were recorded, particularly in areas located to the west of the Dunajec river valley. During this period *Tilia* still increased its amounts in the Jasło-Sanok Depression and the adjacent parts of the Beskid Niski range. The Jasło-Sanok Depression was not affected by regression of lime until ca 4000 BP, and the Beskid Niski range even longer, until ca 3000–2000 BP. Since ca 1500–1000 BP the taxon has been found only occasionally in the area of Polish Carpathians.











