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Review

A Review of the Characteristics of Small-Leaved Lime (*Tilia cordata* Mill.) and Their Implications for Silviculture in a Changing Climate

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Abstract: *Tilia cordata* Mill. is a minor European broadleaved species with a wide but scattered distribution. Given its scarcity and low value in the wood market, it has received little attention from researchers and forest managers. This review summarizes the main aspects of *T. cordata* ecology and growth. Its main limiting factor is its need for warm summer temperatures to ensure successful seed production. It has a height growth pattern relatively similar to that of *Acer pseudoplatanus* L., with a slight delay in the early stages. Yield tables report great productivity, especially in eastern Europe. *T. cordata* used to be a major species in Europe, in contrast to its present distribution, but it is very likely to receive renewed interest in the future. Indeed, with the potential change of competition between species in some regions and the need for important diversification in others, *T. cordata* may play an important role in forest adaptation to climate change, especially owing to its wide ecological tolerance and its numerous ecosystem services. It is necessary to increase our knowledge about its regeneration and its responses to environmental and silvicultural factors, to establish clear management recommendations.

Keywords: *Tilia cordata*; ecology; growth; silviculture; climate change

1. Introduction

Climate change is recognized as the major cause of current changes in the distribution of some species [1–3]. Given their longevity and their economic value, trees are an important concern, and studies of the effects of climate change on forests are increasingly prevalent in the literature. In temperate Europe, these effects are already noticeable in the loss of growth and vitality of some tree species as a result of such extreme climatic events as summer droughts and heat waves [4,5]. Pest and pathogens outbreaks, increasing windthrows, changes in fire regimes or more frequent floodings are also impacts that affects forests [6]. In addition, western European forests and particularly their interspecific compositions appear to be poorly prepared for these numerous effects. Indeed, forest management in recent centuries has greatly influenced the composition of the vegetal communities in favor of a small set of tree species with a high commercial value, such as *Picea abies* (L.) Karst., *Fagus sylvatica* L., and *Quercus* spp., which have been shown to be potentially vulnerable to the effects of climate change [7–9]. Important shifts in the specific composition of European forest are thus expected to occur in the 21st century [10].

Within this context, it seems worthwhile to pay more attention to indigenous scattered European broadleaf taxa such as *Acer*, *Alnus*, *Betula*, and *Tilia*. These species may gain ecologic and economic

value in the future, and by increasing forest diversity, lower the risks from climate uncertainty. Among these species, *T. cordata* may be valuable in a changing climate for its broad ecological amplitude, drought tolerance, and numerous silvicultural benefits that it brings to mixed stands [11].

Among the four species of the genus *Tilia* that grow naturally in Europe, the small-leaved lime (*T. cordata* Mill.) is the most widespread [12] in temperate woodlands. Although it is a relatively rare and scattered species, it was very abundant in the past [11]. Indeed, its relatively good shade-tolerance and its mid- to late-successional character in forest dynamics [13] made it originally a co-dominant species of temperate primeval woodlands of central and Eastern Europe. Because of its scarcity and its low economic value in the current wood market, the ecology and silviculture of *T. cordata* have so far been poorly documented in the literature, especially in Western Europe. However, it is very likely that *T. cordata* and other secondary species will be of increasing interest to the scientific community and forest managers in the future.

The main objective of this review is to summarize the existing knowledge of different aspects of the ecology of *T. cordata*. The issues that will be addressed are site requirements, life strategy (light requirement, growth dynamics, regeneration, phenology, health, and robustness), and natural distribution, as an ecological synthesis. For each topic, we will try to describe the main environmental factors that may affect its variability. Subsequently, the originality of this review is to deduce from this information the response of *T. cordata* to the changing environment, and its future perspectives with climate change. Using this approach for *T. cordata*, we also intend to draw attention to the potential of many scattered tree species by highlighting the opportunities that they represent for the future of forest management.

2. Site Requirements

2.1. Temperature

T. cordata is classified as a warmth-demanding species [14,15]. Relatively high temperatures (>15 °C) during the growing season are indeed required for the successful production and development of fertile seeds [16]. Its critical maximum temperature is estimated to be 44 °C [12], and generally, high temperatures are not a problem if the water supply is sufficient. *T. cordata* also has high cold tolerance. This tolerance varies during the year, and the resistance tends to naturally increase after the first cold days to a maximum in January and February [17]. Till [17] showed that dormant shoots can support temperatures down to −34 °C without damage. The critical minimum temperature varies between −45 °C and −48 °C, depending on the region [11]. Because of its late budding, *T. cordata* is rarely damaged by spring frosts. In the same way, the early leaf fall [18,19] prevents early frost damage. Like other tree species, the response of *T. cordata* to temperatures is closely related to the water supply. Generally, if annual rainfalls are greater than 550–600 mm, the water supply becomes secondary in the determination of the distribution of *T. cordata* and temperatures have a greater influence [11].

2.2. Water Supply

T. cordata is a drought-tolerant tree species. It is weakly, or not at all, affected by short periods of drought [14,18,20,21]. Nevertheless, in the Mediterranean region, where annual rainfalls are less than 500 mm and evaporation is high, *T. cordata* is still often restricted to north-facing slopes, ravines, and zones with a good water supply [11]. *T. cordata* is considered a mesophilic species [19,22] with a good tolerance to dry soils. In a study of the characteristics of tree species niches in Denmark, Lawesson and Oksanen [23] observed that *T. cordata* could tolerate very wet soils as well as very dry ones. This outstanding tolerance can be explained by different factors. Its water use efficiency is very effective [24]. It develops deep roots [18] and has economical water use, notably because of the great sensitivity of its stomata [25]. According to Pigott [26], the drought tolerance of *T. cordata* could also be linked to an association with the mycorrhiza *Cenococcum geophilum* Fr. However, even if a brief period of limited water supply does not affect its survival, it has been shown that it can significantly reduce its radial

and height growth, especially in summer [27]. Moreover, for successful germination, seeds of *T. cordata* require at least 15% moisture content in the litter [27]. Thus, throughout Europe, *T. cordata* is more abundant in regions where soils remain moist in spring and summer.

Even though *T. cordata* shows flood-induced reduction in photosynthesis [28,29], it tolerates short-term flooding as well as *Fraxinus excelsior* L. does, and is thus less sensitive than *F. sylvatica* or *A. pseudoplatanus* [30–32]. In slight contrast to this ranking, Glenz *et al.* [33] classify its flooding tolerance as low (rank 2 on a scale with 5 as the most tolerant) due to its poor morphological and physiological adaptations (e.g., no development of lenticels, no aerenchyma tissues) whereas *F. excelsior* is classified as intermediate and *Salix* species as high (4) or very high (5).

Soil texture, structure, and depth are three parameters that directly influence soil water capacity. Given the tolerance of *T. cordata* to water supply variations, it makes sense that it will be found across a very broad range of these factors. As regards soil texture, it can be found on soils with a high content of clay, as well as on very sandy or loamy soils, or even on screes and soils with a very high proportion of pebbles [12,18]. Weissen *et al.* [19] only exclude it from peaty soils. Its preferences, though, are for intermediate, well-balanced soils [15,34]. The growth of *T. cordata* is optimal on relatively deep soils (>0.6 m) [11,35], but it can grow on more superficial soils, like steep slopes, cliffs, or ravines.

2.3. Soil Nutrients

A particular key strength of *T. cordata* is its tolerance to a wide range of soil fertility. It grows successfully on a soil acidity ranging from pH 4 to 8. However, neutral to basic soils, wherein the pH rises above 5 or 6, seem to be optimal [12,19,22]. Pigott [18] reported that several experiments showed a significant increase in the growth of *T. cordata* when the soil was enriched with nitrates or potassium. However, no response was observed when phosphates were added. It also reacts positively to sites with a high calcium level [36].

3. Life Strategy

3.1. Light Requirements

Because of its ability to grow spontaneously under the cover of light-demanding tree species, *T. cordata* can be classified as a post-pioneer or mid-to late-successional species. *T. cordata* is shade-tolerant and is often qualified as a semi-shade tree species [18,22,35]. According to the scale tolerance of Niinemets and Valladares [37], *T. cordata* has a shade-tolerance score of 4.18 (where 1 is very intolerant and 5 is very tolerant) and is located between species like *A. pseudoplatanus* (3.73) and *F. sylvatica* (4.56). It has been shown that the shade tolerance of *T. cordata* in pure stands is due to a specific pattern of carbon and nitrogen allocation to the leaves [38]. Depending on the study, the described shade tolerance of *T. cordata* will vary from moderate [39] to high [18]. This difference in perception may be due to the fact that the tolerance varies with the growth stage of the tree and the geographical situation [40]. Indeed, as for other species, the light requirement of *T. cordata* increases with age [27]. When well established, it reacts very positively to a gradual opening in the canopy. Furthermore, Pigott [18] reported that seedlings need more light in the third and fourth year for successful regeneration, even if they are able to survive under a dense canopy. In the north of its distribution area, *T. cordata* is considered shade intolerant by some authors due to its difficulty in surviving under the dense canopy of *P. abies* [40,41].

3.2. Growth and Productivity

Even though *T. cordata* is widespread in Europe, very few investigations providing quantitative details on its growth and yield are reported in the literature. So far, no analysis is available summarizing the growth pattern of this species over a larger geographic range. Most report observations from local situations and under specific ecological conditions.

The life span of *T. cordata* can reach up to 1000 years [42,43], with the first signs of rot inside the trunk at around 250 years. Upon the death of the tree from generative reproduction or after coppicing, stools often show emerging sprouts and thus ensure a much longer lifetime and fast height growth during the first years [42]. Together with its shade tolerance, the longevity of *T. cordata* even under low growth is the key characteristic to understand the good general survival probabilities of this species in forest succession models [44]. Despite its high survival rate under varying shade conditions, the following sections examine the growth dynamics of *T. cordata* under full light within a timespan often considered in forestry.

3.2.1. Height Growth

Larger scale investigations of the height growth of *T. cordata* in Europe all report one common characteristic (Figure 1a,b): rapid height growth when young (15–25 years), which then slows. For instance, on sites studied by Böckmann [45] and sites studied by Magyar [46] where seeded or planted *T. cordata* grew best, it reached 11.7 m and 13.5 m, respectively, after 20 years (top height of 100 thickest trees· ha^{-1}); while on the poorest sites, the lowest heights were 4.9 m and 6.5 m, respectively. Site indices after 100 years varied between 36 m [45] and 20.7 m [46]. Height growth models from Poland and Russia reported by Czuraj [47] and Tyurin *et al.* [48] differ slightly with respect to early growth; the trees are shorter after 20 years (Figure 1c). As an extraordinary exception, Shvydenko *et al.* [49] report much higher stand heights for Ukraine and Moldavia, with *T. cordata* stands reaching up to 52.9 m after 100 years. Unfortunately, no more information has been provided on the underlying site conditions.

Compared with *F. sylvatica* (Figure 1d), *T. cordata* grows faster when young (<20–40 years) and shows a general height growth pattern similar to *A. pseudoplatanus* [50], *F. excelsior* [51], *Alnus glutinosa* (L.) Gaertn. [52], and *Prunus avium* L. [53]. However, in contrast to the latter species, the height growth of *T. cordata* is less pronounced in its early years. Thus, among these fast-starters, as valuable broadleaved species [54], *T. cordata* exhibits a slightly shorter height increment, with maximum values on its best sites of approximately 0.7 m· years^{-1} after 10 years.

T. cordata is thus overgrown at early ages by very fast-starting species. Therefore, it has been used in silvicultural systems in mixed stands with other valuable tree species as an understory species for shading valuable trunks to prevent the sprouting of epicormics. In mixed stands with *F. sylvatica* or *Quercus*, *T. cordata* serves the same purpose, but it needs special tending and coppicing at early ages to not compete too much with the crowns of slow-growing *F. sylvatica* and *Quercus*.
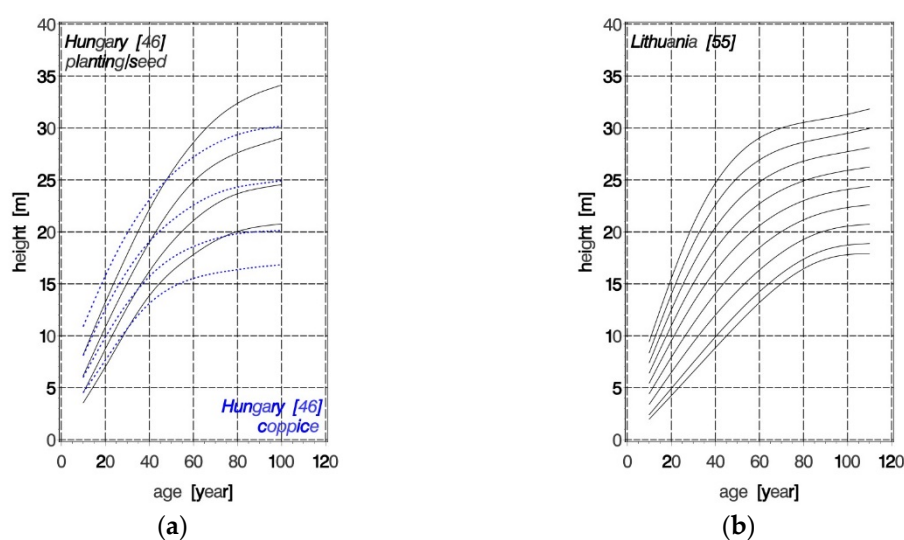

Figure 1. *Cont.*
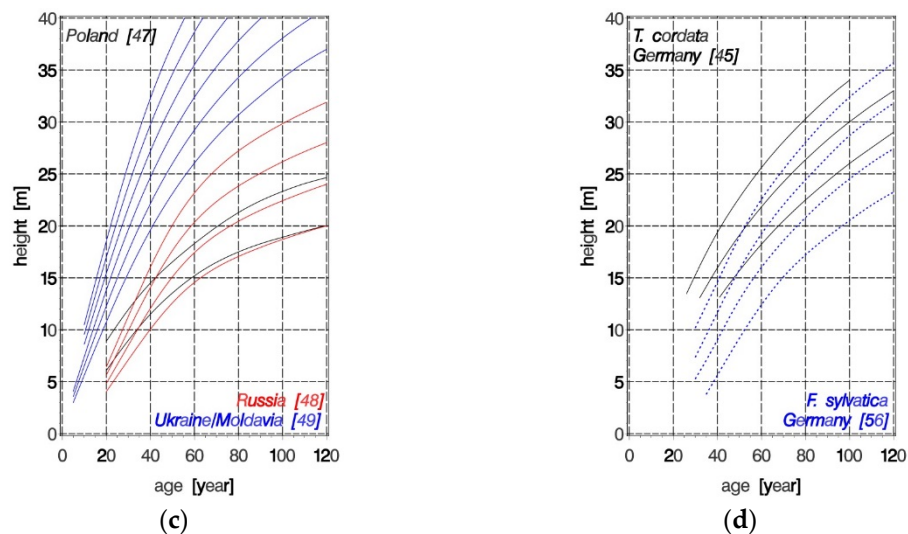
Figure 1. (**a**) Comparison of height growth of *T. cordata* originating from generative (black, solid) *vs.* vegetative (blue, dotted) regeneration (Hungary [46]); (**b**) *T. cordata* from Lithuania [55]; (**c**) *T. cordata* from Poland (black, solid) [47]; Ukraine/Moldavia (blue, solid) [49]; and Russia (red, solid, values not displayed: 140–200 years) [48]; (**d**) *T. cordata* (black, solid) [45] *vs. F. sylvatica* (blue, dotted) [56], both Germany.

However, other factors influence the height growth of *T. cordata*. The Hungarian yield tables differentiate stand growth originating from generative propagation and sprouting from stools. *T. cordata* trees sprouting from stools appear to be taller at young ages, but do not reach final tree heights similar to those from seeds or planting. Such a growth pattern is known for other species (e.g., black alder [57]), but for *T. cordata*, it has only been quantitatively described in Hungary.

A similar pattern of height growth has been reported from several local and small-scale investigations (e.g., Rossi [58]) from Zürich, Switzerland. After 40 years, *T. cordata* reached a dominant height of 21 m, matching the values of the best site index from Böckmann [45]. This is also in line with dominant heights of 10–12 m from 25-year-old *T. cordata* plots in Thuringia, Germany [59] or Erteld [60], values higher than those for admixed *F. sylvatica* in the stands measured. In addition, in young long-term experimental plots in the Czech Republic, *T. cordata* was confirmed to start with fast height growth; under highly varying site conditions it reached mean heights of 8–16 m after 16 years.

Despite some obvious common characteristics, there is some variability that cannot be explained. For instance, it remains unclear whether the differences in height growth between curves from continental Europe [47,48] and European regions with a more oceanic climate [45] can be attributed to contrasting site conditions or are simple artefacts. Furthermore, to date, there are no quantitative investigations of the genetic influence on height growth and there is little quantitative information on the variability over time. There is no analysis of the reasons underlying such phenomena, like silvicultural prescriptions and their changes over time, unbalanced datasets, or statistical smoothing methods applied to the data, so that the underlying causes can only be hypothesized. Finally, none of the models mentioned so far integrate quantitative climatic measures in their influencing factors.

3.2.2. Diameter Growth and Crown Dimensions

The diameter growth of rare species is often recorded from accidental observations on some single individual trees. For instance, Koop [61] listed advancing diameter growth in unmanaged stands of Białowieża National Park, Poland, starting from 15 cm by age 50 to 85 cm by age 400 years. Radoglou *et al.* [12] reported from forests in the same park a maximum diameter at breast height of 2 m. On the best sites (top height of trees: 34 m at 100 years), as described by Böckmann [45], a diameter at breast height of 54 cm can be expected. Similar values from Poland are 39 cm at a mean tree height

of 23 m [47]. However, in forest management, controlling diameter growth is within the focus of silviculture, and thus, it is of special interest how much and when diameter increments should be reduced or sped up in order to reach production objectives. So far, no such production objectives are available for *T. cordata* with, for example, quantitative specifications of the target stem density, final quality, clear bole length, rotation time, or final target diameter, as are already calculated for other rare broadleaved species (e.g., [51] for *F. excelsior*, [54] for *P. avium*, and [54,62] for *Betula pendula* Roth. and *Castanea sativa* Mill., [52] for *A. glutinosa*).

The crown dimensions of trees have often been used in arboriculture and forest modeling to graphically display trees in open space or to calculate production objectives. *Tilia* species used for urban forestry in Copenhagen [63] reached an average tree height of 20 (7.5) m, a diameter at breast height of 55 (14) cm, and a crown diameter of approximately 14 (5) m by age 100 (15) years. In Southern Germany, a sample of 153 *T. cordata* trees measured in urban areas had a mean diameter of 36.6 cm and a crown diameter 8.4 m at a mean age of 70 years [64]. Fifteen-year-old *Tilia spp.* measured across a large variety of sites in New Haven (north-eastern US) had slightly diverging values of 9.5 m in height, 21.9 cm in diameter at breast height, and 7.1 m in crown diameter [65]. However, urban trees have different physical dimensions and specific allometry because of difficult water supply and extreme climatic conditions. Thus, the transfer of such findings to forest management is not appropriate [50,66]. To date, only Savill [67] has provided a simple allometric relationship for *T. cordata* from closed forest stands; large trees exhibit a ratio D/d (crown diameter/diameter at breast height) of 15.

3.2.3. Volume Growth and Productivity

Information about volume growth and productivity of *Tilia* is sparse and not well structured. For Germany [45] and Poland [47], yield tables display the range of volume growth depending on the site conditions found within specific geographical limits. They show, as for height growth, early culmination of current annual volume increment (CAVI), with values range of 6 to 20 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} at an age of 30 to 45 years, according to site quality. Mean annual volume increment (MAVI) shows its maximum between 5 and 11 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} around 60 to 100 years respectively.

Other dispersed local observations on stand volume, CAVI, and MAVI reported by other authors of Sweden, Lithuania, and Denmark [67], Slovakia [68], Poland [36] and Russia [48] (Table 1) are generally consistent with the structured information of the yield tables.

Table 1. Volume growth and productivity values for *Tilia cordata* in Europe.

Yield Tables		
Country [Reference]	**Parameter**	**Range of Value**
Germany [45]	Range of max CAVI and corresponding ages	11.9 to 20.2 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} 30 to 45 years
	Range of max MAVI and corresponding ages	10 to 11.5 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} 60 to 100 years
Poland [47]	Max CAVI and corresponding age	6.2 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} at 35 years
	Max MAVI and corresponding age	4.7 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} at 35 years
Local Observations		
Country	**Parameter**	**Range of Value**
Sweden, Lithuania and Denmark [67]	CAVI and corresponding age	10 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} at 35 years
Slovakia [68]	CAVI and corresponding age	5–11 m$^3 \cdot$ha$^{-1} \cdot$years^{-1} at 30 years
Poland, unmanaged forest [36]	Standing volume	760–860 m$^3 \cdot$ha^{-1}
Russia [48]	Standing volume	594–810 m$^3 \cdot$ha^{-1} at 100–200 years

CAVI: current annual volume increment; MAVI: mean annual volume increment.

Comparing volume productivity with *F. sylvatica* [56], the following main characteristics are apparent: CAI and MAI culminate much earlier than for *Fagus*, similar to height growth. Furthermore, the stocking volume and total volume productivity of *T. cordata* are higher at ages <80 years compared to *Fagus* but lower at later stages of stand development. There is no significant difference between the total volume productivity of *T. cordata* and *A. pseudoplatanus* [50]. As height growth differs between these species, diverging patterns of tree diameter growth and stem density dynamics can be expected.

Even though such scattered information is commonly found, more model building is needed for forest growth and yield tables or simulators. No investigation has so far been done on thinning intensity or grade on tree diameter or stand volume productivity, as has been done for other rare broadleaved species. However, from the findings on height growth reported above, the general pattern is highly likely that early culmination of height growth is paralleled by good crown reaction to early thinnings, and a reduced response at older ages and thus reduced volume productivity. At this time, it is not possible to quantify when such a transition and which thinning intensity or level of silvicultural interventions will finally lead to such an expected reaction.

3.3. Regeneration

Natural regeneration of *T. cordata* can either occur from generative or vegetative reproduction. The requirements for successful generative reproduction are numerous, making it very difficult. In contrast, vegetative reproduction is very common and is fully part of the life strategy of the genus *Tilia*, especially in marginal climatic conditions for seed production.

3.3.1. Generative Reproduction

Tilia are considered to be hermaphroditic [18], but Tal [68] has shown that the male gender seems to dominate. *T. cordata* seems therefore to be andromonoecious, meaning that it can carry either hermaphroditic or purely male flowers. However, male flowers are rare, and their frequency appears to decrease during the flowering period. Their development is largely influenced by light, drought, and, eventually, frosts [68]. Nectar production is dependent on the temperature reaching at least 15 °C. The intensity of flowering varies among years, but the duration of flowering seems to remain constant, as is the case for other late species. Flowers are undoubtedly entomophilous. They are yellowish-white and stand out from the dark green leaves, which makes them very visible during the day. In addition, they emit a powerful fragrance even at night. Therefore, *T. cordata* attracts a wide variety of pollinators during both the day and the night, especially in the upper part of the crown where flowers are more abundant [11,18,68]. *Tilia* flowers and pollen are traditionally associated with bees, but flies and moths are also very common visitors [69]. Pollen of *T. cordata* is also present in the air around the tree. Wind pollination is therefore possible [69], but the main vector of pollination is insects.

Fertilization is optimal between 15 °C and 22 °C [16]. With temperatures less than 15 °C, the pollen tube does not grow and is thus not able to reach the embryo sac, making seed production impossible. The fruit of *T. cordata* is a greyish, small, spherical capsule. Fruits generally contain one seed, but sometimes have two or none [68]. Generally, the percentage of empty fruits is estimated at around 40%, but observations suggest some influence of climate on this proportion. For example, it varies from 40% to 95% in south and central England to 85%–100% in northern England [18]. In the north of its distribution, the production of enough seeds to establish natural regeneration is thus limited to exceptionally warm summers [16]. In addition, in cold climates the proportion of empty capsules also increases with age. *Tilia* trees produce seeds almost every year, but the number of seeds fluctuates from year to year [68]. Murachtanov (1981) estimates the production at 1,000,000 seeds·ha^{-1} in mast years, 500,000–700,000 seeds·ha^{-1} in medium years, and 150,000–300,000 seeds·ha^{-1} in poor years. Mast years, however, are very infrequent. This variation in seed production intensity among years seems to be induced not by climate fluctuations but rather by nutrient availability and an economy-of-scale strategy [70], both described as important factors explaining the masting behavior of trees. Fruits generally mature and fall in autumn, but some can remain on the trees for the winter. Wind

is the main vector of seed dispersion. Fruits are coupled with a long bract that acts like a wing and induces spinning during the fall; this slows the fall to 0.9–1.1 m·s^{-1}. Therefore, if the tree is about 30 m high, some fruits may be transported up to 300 m from the tree. However, fruits generally fall very close to their parents, even in open areas. Seeds could also be dispersed by water, although it is very rare [11]. Fruits and their bracts can float for a long time and can be carried by streams for relatively long distances (up to 30 km). If seeds do not germinate in the following spring, their germination can take several years [18,71]. Generally, they do not germinate before two years in natural areas. The causes of this long dormancy are the toughness of the pericarp, the tegument's impermeability to oxygen and water, and the embryo's dormancy, which requires 14–18 weeks of chilling conditions to be broken [72,73]. Seeds can germinate from 2 °C, but the optimal temperature for germination is above 20 °C. Light is not necessary for germination [74].

3.3.2. Vegetative Reproduction

The relatively high occurrence of *Tilia* trees with more than one main stem can be explained by their vegetative origin. *T. cordata* strongly spreads through clump shoots and root suckering. In south-western Russia, almost 80% of young *Tilia* trees are derived from vegetative reproduction, and this percentage peaks near 100% in north-eastern Europe [75,76]. In the Białowieża Forest in Poland, most of the old *Tilia* trees have offshoots growing from the base of the trunk [77]. The sprouting vigor does not seem to decrease with time [18], and sprouts also grew very frequently from the root collar or, after cutting, from the tree stump [78]. One sprout can replace an old or dying parent tree and thus prolong its life, even after the destruction of its trunk. In contact with the soil, branches may also develop roots and vertical shoots. The exceptional ability to vigorously reproduce vegetatively enables *Tilia* populations to exist near the limits of their natural range and to compete effectively against *F. sylvatica* in coppices. The process is a survival strategy and is probably the result of a long history of adaptation to survival in a multispecies forest [78].

3.3.3. Hybridization

Several natural hybrids of *T. cordata* exist, but the most common is *Tilia × vulgaris* Hayne (*T. cordata × Tilia platyphyllos* Scop.), which is often planted in western Europe, particularly in urban environments [22]. This hybrid is also synonymously named *Tilia × europae*. The time lag between the flowering of *T. cordata* and *T. platyphyllos* makes their interbreeding relatively rare in natural areas, but in some particular conditions, such as abrupt slopes with high elevation differences on a short distance, hybridization is possible [11]. The distinction of *T. vulgaris* among the other *Tilia* species is very difficult given the presence of both parents' anatomical features [22]. *T. vulgaris* appears to not be completely sterile, but it has very poor fructification [11]. More specific studies would help to correctly understand and estimate the full scale of the phenomenon in natural areas, and its frequency and consequences. When they grow close to each other, natural hybrids of *T. cordata* and *Tilia tomentosa* Moench can also be observed (*T. × juranyana* Simonk) [11].

3.4. Phenology

The phenology of *T. cordata* is highly variable, and it depends primarily on the environmental conditions. When compared with other tree genera like *Fagus* and *Acer*, *T. cordata* can be considered to have late bud burst and leaf unfolding and early leaf fall [79,80]. Usually, bud burst occurs in mid-April and the first developed leaves appear approximately 5–10 days later, which is a very short period [18,79,80]. These spring phenophases are strongly correlated with air temperature, particularly the accumulation of temperatures [79,81]. In the study of Wesołowski and Rowiński [80] in Białowieża National Park (Poland), the sum of the temperatures greater than 0 °C from March was the best predictor of the budbreak date. This sum was two times greater than for *Corylus avellana* L., one of the earliest species. Caffarra and Donnelly [82] show that *T. cordata* requires a long chilling period (on average 40–65 days) in winter to break bud dormancy and is sensitive to light intensity. The flowering

of *T. cordata* also seems to be regulated by the accumulation of temperatures [11] and is thus delayed at higher altitudes and latitudes. In each inflorescence, the terminal flower of the cyme opens first when the weather is warm and is followed by the others at a one-day interval [16]. Usually, flowering occurs 3 months after budburst [21]. *T. cordata* generally flowers at the beginning of June in the north of Italy; in early July in France, Germany and the south of England; and in August at the northern limit of its distribution [21,83]. From south to north, a delay of about 50 days can be observed. Generally, in an open, unshaded area, trees can start flowering between 12 and 20 years of age, whereas in more dense woodlands, the trees must reach 25–40 years of age [18]. According to Weissen *et al.* [19], the optimum age for good fructification is beyond 40–50 years.

Leaf coloring starts in the second half of September, and leaf shedding usually ends around late October or early November [55,79,84]. According to the observations of Schieber *et al.* [79], there is a significant positive correlation between the autumnal coloration of the leaves and the cumulative precipitation from May to August. Given its late budding and early leaf shedding, *T. cordata* has a very short vegetation period.

3.5. Health and Robustness

Because of its high shade tolerance when young and its extremely efficient vegetative reproduction, *T. cordata* can be considered as a competitive species. However, the fact that *T. cordata* is relatively rare, almost exclusively present in mixed stands, and is often dominated, indicate a lower competitive ability. Even if other reasons, notably anthropogenic ones, are involved, *T. cordata* is often supplanted by *F. sylvatica*, and is thus favored in regions where the vitality of *Fagus* is reduced by frequent late frosts and droughts [11] or at sites with constraints such as sunny slopes or pebbly soils [85]. In Scandinavia, *T. cordata* is mainly limited by *P. abies*, which is much more competitive and can easily perpetuate its dominance once established. The light requirement of *T. cordata*, especially for flowering, is the principal factor that limits its competitive ability. Pigott [18] reports that herbaceous flora only impacts young seedlings in dense stands of *Mercurialis perennis* or *Aegopodium podagraria*.

T. cordata takes advantage of the absence of serious pathogens and pests. Generally, damage and disease caused by insects or fungi do not endanger the survival of the species in woodlands. Among the most widespread parasites, the bites of some insects, such as mites (genus *Eriophyes*) and midges (*Contarinia tiliarum* or *Dasineura tiliamvolvens*), induce gall development on the leaves and can slightly weaken the trees [18,34]. In European Russia, the leaf miner *Phyllonorycter issikii* specifically attacks *T. cordata* and has a significant negative effect on its productivity and reproductive capacity [86]. *T. cordata* is also susceptible to *Phytophthora* spp. fungi [18], which could be a threat given their increasing frequency, particularly in Mediterranean and Atlantic regions [87].

Seedling trees of *Tilia* that grow under favorable conditions, even those more than 150 years old, generally do not present any decay. In contrast, heartwood decay can already appear at 60–70 years of age in trees regenerated by sprouting [11].

T. cordata is not usually a preferred browse choice for cervids [12]. Its attractiveness is relatively moderate and much lower than that of *P. abies*, *F. excelsior*, *B. pendula*, or most fruit trees. Different studies have shown that, except in case of very high deer density [88,89], *T. cordata* is very rarely browsed and is moderately susceptible to bark stripping by deer [18,90]. In conclusion, considering tree health, *T. cordata* is a very interesting species.

4. Genetic Resources

There have been very few studies on the genetics of *T. cordata* [91,92]. According to Logan *et al.* [92], this is partly due to the limited number of useful molecular markers available. Nevertheless, given the similar morphological traits within the genus *Tilia*, genetic techniques might be required to differentiate *Tilia* species and their natural hybrids [11]. The research led by the United Kingdom on *Tilia* populations has shown that microsatellites markers are a very effective tool to successfully distinguish *Tilia* species and to study their variability. The study confirms that both *T. cordata* and

T. platyphyloss are diploid, outcrossing and have a high genetic diversity within and between species. This high diversity has also been observed across different populations in Europe by Phuekvilai [93]. In Europe, the genetic diversity of *T. cordata* seems to decrease as latitude increases. This higher genetic diversity in southern Europe could be explained by the favorable climate and stable environments during the glacial period [93]. Still, the genetic diversity of *T. cordata* is currently threatened due to large distances between fragmented populations [91]. Myking [94] classified the genetic resources of *T. cordata* as vulnerable, assuming a significant decrease of the genetic variation within its populations. Many concerns have led to this classification. Given its scattered distribution and its limited seed dispersal capacity, the gene flow of *T. cordata* is relatively limited. Its post-glacial migration rate is estimated to be 5–500 m· years^{-1} according to pollen records [95], which is much slower than other tree species, such as *Alnus* sp. (2000 m· years^{-1}), *P. abies* (80–2000 m· years^{-1}), and *Acer* sp. (500–1000 m· years^{-1}). In addition, the selective removal of *Tilia* sp. in the past by humans may have increased the risk of genetic erosion in the future [14,91]. In continental Europe, most countries set up seed stands and a genetic conservation program for *T. cordata* [96]. At least 44 seeds orchards (covering 136.7 ha) and more than 550 ha of selected seeds stands are present in Europe, mostly in Poland, Germany, Czech Republic and Serbia [97].

5. Distribution

5.1. Natural Areas

T. cordata is one of the most widely distributed broadleaved tree species of European woodlands [18] (Figure 2). It is mainly referred to as a sub-oceanic to sub-continental species. In northern Europe, *T. cordata* occurs up to central Sweden and the south of Norway and Finland, which corresponds to about 63° N [18,91]. This limit is associated with the July isotherm for mean daily maximum temperature of 19–20 °C [16,18]. Beyond this, the harsh climate, especially the low summer temperatures and the frequent frosts [27], impedes its development and its production of fertile seeds (nectar production, fertilization) [16]. Southwards, *T. cordata* extends to the northern Iberian Peninsula and northern Greece. Its distribution in the Mediterranean region is mainly limited by summer droughts, low air humidity, and very dry soils [12,24]. From west to east, *T. cordata* expands from Northern Ireland to beyond the Urals, up to the Irtysh River in central Russia, where its limit follows the border of the Russian steppe until it reaches the Black Sea [18,71]. The characteristic low precipitation of the steppe is probably the major obstacle to its eastward expansion [18]. Of course, *T. cordata* can also be found in some outlying localities with a favorable local climate like the Caucuses and Crimea.
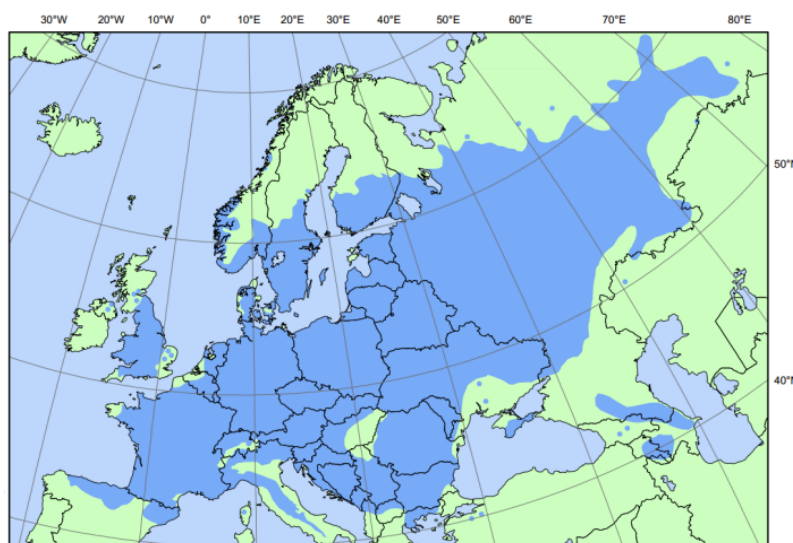

Figure 2. European distribution of *T. cordata* [91].

5.2. Local Distribution and Abundance

Following the National Forest Inventories, *T. cordata* is only present in less than 5% of the forests [66], but its abundance varies strongly across Europe [91]. The local abundance is mainly the result of interactions among three factors: the natural environment (bioclimatic and local site factors), competition, and human management. Following a gradient of continentality, *T. cordata* is very scattered in Western Europe (France, Belgium, Unites Kingdom, Denmark), scattered in central Europe (north-east France, central Germany, Switzerland,) and tends to be more common in eastern Europe (Austria, Poland, Romania, Hungary, Croatia, central Russia, *etc.*) where the climate seems to suit it better and it takes advantage of the relative weakness of *F. sylvatica* in such bioclimatic conditions [39]. Indeed, the regions where *T. cordata* is the most common are characterized by annual precipitation values of 500–800 mm, with a slight peak in the growing season [24]. In the Mediterranean region, where annual rainfall is less than 500 mm and the evaporation is high, *T. cordata* is almost exclusively present above 200 m on north-facing slopes, ravines, and zones with a good water supply [11]. It is thus mostly present in mountainous areas, as illustrated by its locations in Italy and Corsica [18].

In the bioclimatic optimum of *F. sylvatica*, and especially in Western Europe, *T. cordata* is most abundant on marginal sites as stagnogleic brown soils [11] or xerothermic sites as south-facing slopes [85]. Concurrently, *T. cordata* is most frequent in Eastern Europe where forests have been less impacted by human management. Indeed, foresters generally favor *F. sylvatica*, *Quercus* sp. and conifers to the detriment of other secondary species as *T. cordata*, considered as low value species [85]. However, the ability of *T. cordata* to produce coppice shoots has allowed it to survive in mixed stands and in some favorable sites to form pure coppice stands.

6. Silviculture

6.1. Mixed Stands and Ecosystem Services

T. cordata is then rarely found in pure stands [91] but it is a frequent component of mixed stands, scattered in groups or as irregularly dispersed single trees. On subhumid loamy soils of Western Europe (Belgium, France), it forms part of the canopy of mixed forests dominated by *Quercus robur* L., *F. excelsior* and *A. pseudoplatanus*. On better soils, *T. cordata* is associated with a set of companion species (e.g., *A. pseudoplatanus, B. pendula, P. avium, Sorbus sp.*) in secondary forests dominated by *Quercus* sp. and *Carpinus betulus* L., resulting from the alteration of *F. sylvatica* potential climax by forest managers [39,85]. In Eastern Europe, *T. cordata* can dominate the canopy composition, often associated with *Quercus* sp. and *C. betulus* [13]. Such mixed stands can be from silvicultural systems that integrate *T. cordata* as a shading species that is able to grow in the shade of other species. *T. cordata* is helpful for controlling understory light and the development of the herbaceous layer, for natural pruning of the associated species. Associated with *Quercus* sp., *T. cordata* can prevent the onset of epicormic shoots by shading the *Quercus* trunk [98].

T. cordata is also helpful as an admixed component for improving nutrient cycling. Its leaves are rich in mineral elements, and their fast decomposition has a positive and significant impact on the quality of the soil nutrient status, especially in nutrient-poor sites [18,19,35,99]. In comparison with *Fagus*, *Tilia* litter has lower C/N and lignin/N ratios, which makes decomposition faster, and contains more base cations [100]. Litter in a *Tilia* stand has a higher pH, base saturation, and nutrient stock than that in a *Fagus* stand [101]. Adding *Tilia* to a stand might thus reduce litter acidification and increase the fertility of the topsoil. Examples of such mixed stands are reported in several studies across Europe. In Lithuania, *T. cordata* is an admixed but rare species in *Quercus*, *Populus*, *Betula*, and *Fraxinus* stands [55]. Tokár and Bolvanský [102] found that the current annual volume increment of mixed *C. sativa* and *T. cordata* stands was higher than pure *C. sativa* stands. However, no study on true overyielding due to mixing *T. cordata* with another species has been reported so far. On the Ufa-Plateau (Urals) in Russia, *T. cordata* is associated with *Ulmus*, *Picea*, and *Abies* species [27], and in Poland with *Quercus*, *Fagus*, *Acer*, *Carpinus*, *Picea*, *Abies*, and *Pinus* species [36].

The ability of *T. cordata* to root and grow well on screes, steep slopes and ravines makes it a very useful species for soil stability on forested slopes [103]. Its flowers are also a very important source of pollen for bees [18]. Thus, *T. cordata* is an excellent auxiliary species that provides many benefits and considerable services to the ecosystem.

6.2. Timber Production

6.2.1. Basic Wood Properties and Use

Woods of the different species of the genus *Tilia* are relatively similar and are very difficult to differentiate from each other, even at a microscopic level. *Tilia* wood has good technical and aesthetic qualities [11,12,34]. It has a regular, fine structure and a uniform, straight-grained texture that is suitable for veneer. Sapwood and heartwood have the same white-yellowish colour and annual growth rings are very subtle. *Tilia* wood is strong and flexible. Once dried, it is stable and easily workable in every direction, which makes it one of the most suitable woods for hand carving and turning. It is also widely used in musical instrument making and can be used to make small furniture. Its lightness and the fact that it does not affect the taste of food makes it a good choice for crate and box manufacturing. It does not produce splinters, which makes it perfect for tool handles [104]. It is also suitable for veneer and produces a high quality charcoal. *Tilia* wood also reacts very well to THM (thermo-hydro-mechanical process) densification treatment [105]. This process significantly improves its dimensional stability, but reduces its thermal stability. Its main drawbacks are its lack of durability, which makes it unusable for building and outdoor construction and the chemicals it contains that causes problems for pulp production. In short, the lime wood properties are especially suitable for joinery, which needs large faultless timbers.

6.2.2. Bole Forming

In accordance with its minor importance on the timber market, there are limited data published on round wood quality in relation to silviculture. Rossi [58] reported a high percentage of forked trees (36%) among stands analyzed in long-term experimental plots in Zürich, Switzerland (age: 16–39 years). Semaškienė [55] also reports frequent forking and differences in stem quality of *T. cordata* in Lithuanian forests, but without connecting such observations with the previous management regime. However, the literature does not point out any risk of damage to the tree (e.g., due to wind or snow) due to the forks. A longer branch free bole has been found with increasing stem density by Trauboth [59] and Rossi [58]; by approximately 40 years of age, a bole free of dead branches for 6.5 m and free of living primary branches for 8 m has been found. Together with their diameter of 20 cm, such a natural pruning pattern indicates a long-living crown and good shade tolerance, as described above. Potentially, *T. cordata* can easily produce a straight bole free of nodes as needed for joinery.

6.2.3. Plantations

It is not recommended to create a pure *Tilia* plantation in an open area. Indeed, young seedlings of *T. cordata* need protection from direct sunlight. It is preferable to use *T. cordata* as a secondary species in association with other tree species. For example, it can be planted simultaneously with *Quercus* spp. or *P. avium*, or under their canopy after thinning. When planted with other species, a seedling density of 800–1000 seedlings per hectare is recommended to reduce the number of future treatments [34]. *T. cordata* can be planted in this way to diversify an existing pure stand. The localized introduction of *Tilia* trees in shaded areas of pure *Pinus* or *Fagus* stands can appreciably raise incomes while significantly improving the ecosystem quality [34]. However, the canopy has to be sufficiently open to allow the future development of the young seedlings, and one or two light thinnings are thus sometimes needed before planting. Some technical guidelines for recommended treatments are proposed by Coello *et al.* [34]. In Sweden, the conversion of pure stands of *P. abies* to broadleaved

woodland is an important issue, and Löf *et al.* [106] have shown that planting under the canopy of *P. abies* with *F. sylvatica* or *T. cordata* is only effective in sparse stands.

7. *Tilia cordata* and Global Change

7.1. Past Dominance and Decline

Pollen analyses show that, from the beginning of the post-glacial period until the mid-Holocene, *T. cordata* was a major tree species of the European woodland [11,107]. During the Holocene Thermal Maximum, which was a very hot and dry period with summer temperatures at least 3 °C warmer than they are now (between approximately 8200 and 5300 B.P.), its dominance was nearly absolute in eastern Europe [107]. *T. cordata* maintained its co-dominance for 2000 years, and then declined considerably between 4000 and 2400 B.P., depending on the region [11], as a result of both climate cooling, favorable to other species (e.g., *P. abies, F. sylvatica*) and growing human activities. According to Bradshaw *et al.* [7], the southward migration of *T. cordata* in Sweden was also a direct response to the cooling of the climate during the Holocene. This climate-related hypothesis is also proposed by Pigott [11], who explained the regression of *T. cordata* in England as due to lower temperatures causing smaller and less frequent seed production. In Scandinavia, the invasion of *P. abies* at the end of the Holocene seems to have accelerated the southward regression of *T. cordata* and shaped its actual distribution [41,108]. Like other deciduous tree species, *T. cordata* could not compete with the dominance of *P. abies*, mainly because of the insufficient access to light. In central Europe, the expansion of *F. sylvatica* also contributed to the decline of *T. cordata*. Owing to its strong competitiveness, *F. sylvatica* rapidly colonized woodlands, particularly on fertile soils [11]. More recently, another factor is the historical practice of coppicing, which favored *T. cordata* due to its sprouting ability [11]. All these factors have led to a situation that contrasts with the former abundance of *T. cordata*.

7.2. Current Climate Change

Since the beginning of the 20th century, mean annual temperature has increased in Europe, with a higher intensity in the North and the 10 hottest years observed since 1880 all occurred between 1998 and 2015 [109]. Since the three last decades, in central and southern Europe, the frequency of extreme events such as heat waves and droughts is also clearly increasing. All the climatic models forecast the same trends during the 21th century [109], and some predict also an increase of the frequency of wind storms. The scientific community agree about the negative impact of these events on forest trees and on the health of forest stands [6,14,110].

7.3. Impact of Climate Change on T. cordata

A lot of scientific studies focus on recent phenological changes because long time series of observations are available. Therefore, phenological observations and their fluctuations over time are major tools for understanding and forecasting plant responses to climate change [111]. The impact of climate change on the phenology of *T. cordata* has already been observed and some trends can be highlighted. As can be expected, a warmer spring is associated with earlier foliation. Sparks *et al.* [112] estimated that for an increase of 1 °C, *Tilia* foliation advanced by 4–8 days according to the time series observations. In Lithuania, the bud burst and the leaf unfolding of *T. cordata* were advanced by 9.6 and 11.3 days on average, respectively, between 1956 and 2010 [113]. However, the development rate of the leaves remains constant during the study period. These trends have been confirmed in Ireland [114], Estonia [115], and Lithuania [116]. Concerning the autumn phenophases, Juknys *et al.* [113] found that leaf coloring was delayed by 10.1 days and the end of leaf fall by 11.3 days. The growing season was thus extended by 22.7 days. A 1 °C increase delays leaf fall on average by 4.45 days. These observations show that the autumn phenophases, which are very complex, may also be influenced by temperature, contrary to what has been argued in other studies [113,117]. The shifts observed in the phenology of *T. cordata* are, however, smaller than those of other tree species like *B. pendula*

or *C. avellana*, which suggests that the phenological sensitivity of *T. cordata* is not as high as in early season species [116,118]. Moreover, phenological models built by Thompson and Clark [21] show that trees of the same species will respond in different ways and will have different sensitivities to increasing temperatures according to their location and the time of the year when they flower. In their phenological study on *Tilia* populations, Minin and Voskova [119] found that in the north of their study area, spring and winter phenological events tended to happen earlier between 1970 and 2010 by 2–4 days on average, but no tendency was observed in the south. However, climate changes were the same throughout the area. These observations might reflect different adaptive strategies or mechanisms adopted by distinct *Tilia* populations.

Until now, the expected impacts of climate change on *T. cordata* vitality are generally deduced from its biology due to the lack of observations. In comparison with the climatic behavior of most tree species, the high tolerance of *T. cordata* to heat waves or drought events is a significant advantage. Its strong rooting should also limit the impact of windstorms on mature trees.

7.4. Potential Future Distribution

Recently, an increase of the abundance of *T. cordata* in mixed stands seems to be observed across Europe [66,120]. This trend can partly be explained by climate warming in reference to the absolute dominance of *T. cordata* in Eastern Europe during the Holocene Thermal Maximum [95]. Indeed, in the north of its distribution, there is almost no doubt that summer temperatures will have, and probably already have had, a significant positive impact on the frequency of production of fertile seeds [11]. Different models also predict an expansion of the boreal forest northwards and a significant increase of *T. cordata* abundance due to climate change [41,121,122]. In boreal and boreo-nemoral areas, it is likely that *P. abies* and *Pinus sylvestris* L. will suffer from the predicted increase in the summer drought frequency, in favor of deciduous broadleaved tree species. *F. sylvatica*, *Quercus sp.*, *B. pendula*, and *T. cordata* may benefit from the higher temperatures and longer growing season to expand northwards and become more ecologically competitive [121,123]. In the Italian Peninsula, however, climate change could lead to a significant decrease in forest cover, which could greatly reduce *T. cordata* population [124]. It is very important to note that at a smaller scale, climate change should result in a modification of the species abundance rather than a real geographical expansion [125], especially given the limited dispersal capacity of *T. cordata*. Because of this limited ability, it is very likely that the northern expansion of *T. cordata* and its growing abundance in Europe will need to be human-assisted. However, there is currently only limited information about *T. cordata* planting and management. Many countries do not even have recommendations for seed provenance. It is thus essential to improve our knowledge about planting *Tilia* (and also many other scattered species) and the associated risks.

7.5. Opportunities

In most regions of Europe today, there is almost no market for the wood of *T. cordata*. There is thus a very low interest in it, and therefore, *T. cordata* is not subjected to specific management practices. In Eastern Europe, however, *T. cordata* has a higher commercial value, especially outside the distribution area of *F. sylvatica*, where it is widely used for domestic purposes [11]. Moreover, it has been shown previously that *T. cordata* can have great productivity, comparable to or even higher than that of some valuable hardwoods of western and central Europe. Because the wood market is constantly evolving, it is thus possible that the wood of *T. cordata* will have a more prominent market position in the future. With climate change, the supply of some widely used tree species may decrease, and it will be necessary to find other alternatives. It is thus important to promote the better use of the wood of other secondary species. Various products can be developed, along with methods to efficiently gather small quantities of wood. Moreover, with the numerous technological advances in wood manufacturing over the last few decades, the wood quality tends to become less important for the industrial sector.

However, the interest in *T. cordata* is not driven only by commercial interest in wood production. With its numerous ecological services (e.g., soil fertility support, soil protection, biodiversity) and its silvicultural roles (e.g., prevention of epicormics, understory light management), *T. cordata* can be considered as a secondary species of first choice in mixed stands. Moreover, it can make a considerable contribution to forest diversification, which is a major challenge for the future of the forestry. Indeed, increasing tree species diversity is an important adaptation strategy to address climate change, especially considering its uncertainty. The diversity, especially with species as *T. cordata*, that is free of major health problems, can buffer the potential negative impacts of climate change (pests, pathogens, *etc.*) and enhance the forest ecosystem resilience to extreme climatic events [126–128]. At least, the high tolerance of *T. cordata* to heat waves and drought events, and its strong rooting limiting its sensibility to windstorm, minimize the risks of its silviculture in the future.

8. Conclusions

In Europe, *T. cordata* grows in a very wide range of environmental conditions. It occurs on a large range of soils, and its climatic flexibility facing dry or warm events is remarkable. It also provides numerous ecological and silvicultural services and has a real wood production potential. Facing the challenge of the forest management under global change, *T. cordata* presents an opportunity for European forests. Forest adaptation to climate change will require higher diversity and thanks to all its key strengths, *T. cordata* should be favored by forest managers.

Despite this, *T. cordata* is relatively rare in western European woodlands at this time, so there is little interest in its ecology or management and relatively few studies in the literature. However, with a quite low investment, it is possible to diversify and improve the quality of a stand and the incomes generated. Thus, it is essential to improve our knowledge of *Tilia* and other scattered species to better determine their potential.

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