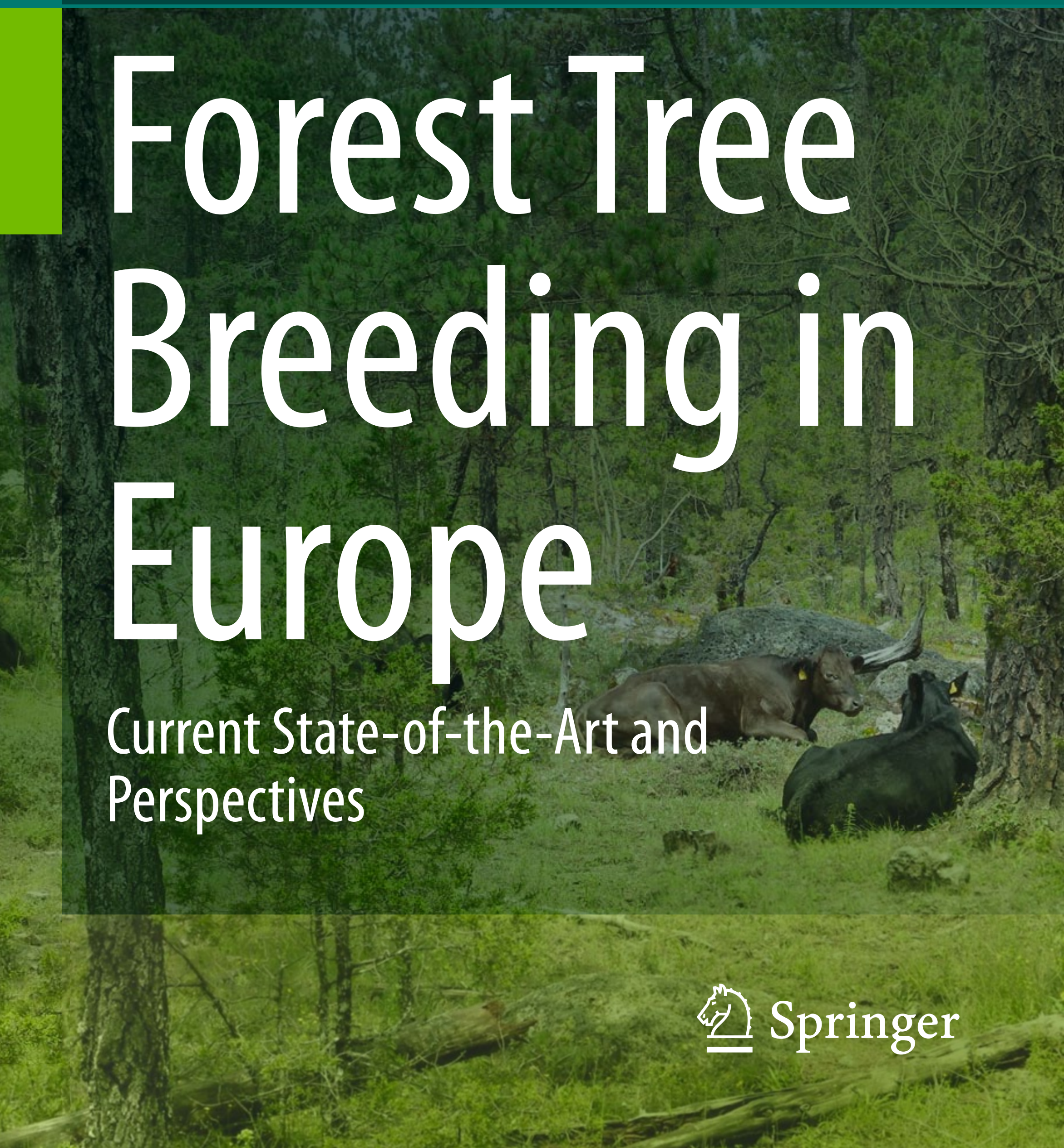
Managing Forest Ecosystems

Luc E. Pâques *Editor*

Forest Tree Breeding in Europe

Current State-of-the-Art and Perspectives



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Aims & Scope:

Well-managed forests and woodlands are a renewable resource, producing essential raw material with minimum waste and energy use. Rich in habitat and species diversity, forests may contribute to increased ecosystem stability. They can absorb the effects of unwanted deposition and other disturbances and protect neighbouring ecosystems by maintaining stable nutrient and energy cycles and by preventing soil degradation and erosion. They provide much-needed recreation and their continued existence contributes to stabilizing rural communities.

Forests are managed for timber production and species, habitat and process conservation. A subtle shift from *multiple-use management to ecosystems management* is being observed and the new ecological perspective of *multi-functional forest management* is based on the principles of ecosystem diversity, stability and elasticity, and the dynamic equilibrium of primary and secondary production.

Making full use of new technology is one of the challenges facing forest management today. Resource information must be obtained with a limited budget. This requires better timing of resource assessment activities and improved use of multiple data sources. Sound ecosystems management, like any other management activity, relies on effective forecasting and operational control.

The aim of the book series ***Managing Forest Ecosystems*** is to present state-of-the-art research results relating to the practice of forest management. Contributions are solicited from prominent authors. Each reference book, monograph or proceedings volume will be focused to deal with a specific context. Typical issues of the series are: resource assessment techniques, evaluating sustainability for even-aged and uneven-aged forests, multi-objective management, predicting forest development, optimizing forest management, biodiversity management and monitoring, risk assessment and economic analysis.

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Treebreedex

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Cover picture legend: Typical scene in the State of Durango where forests are managed by communities known as Ejidos: management is by selective tree removal, clear-felling is not allowed. Animals (ganado) are part of the multiple use system practiced there. (Photo by K.v. Gadow, autumn 2009)

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Chapter 1
Introduction

Luc E. Pâques

Forest tree breeding aims to genetically improve forest tree species

Even if well adapted to their local environment as a result of natural selection pressures, local genetic sources of forest tree species do not necessarily correspond to socio-economic needs and industrial requirements. For example, architectural patterns (e.g. stem form, branching pattern) or internal wood properties (e.g. grain angle, fibre sizes) might not be technically and economically suitable for production of high quality wood end-products. Moreover, local environmental conditions are changing due to new adverse climatic or pest constraints. In addition, human needs are also evolving and new services and products are expected. In conjunction with forest management practices and with adaptation of the industrial process, breeding can be an efficient way to improve forest tree species with regards to current and future environmental and socio-economic needs.

Forest tree breeding basically mimics natural selection through recombination and selection pressure but with two major differences: artificial selection is directional, focusing on socio-economic needs and adaptive requirements, and the selection process is faster.

Forest tree breeding addresses species of economic importance

Tree breeding mainly addresses species of economic importance and for which artificial regeneration, by plantation or by direct sowing of improved varieties, is used for afforestation and/or for reforestation. Improved varieties are thus used firstly in industrial forests, but also in agro-forestry and in some cases for enrichment of local forests. A fast (short rotation) and high and sustained production

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of good quality wood is often an economical and financial priority and high expectations in breeding progress are awaited. On the other hand, high, regular rates of planting with improved varieties then become the driving force of breeding programmes: currently the most active and innovative breeding programmes exist across Europe and in the world only for species which are either heavily planted or have a high timber value. In Europe these include: Scots pine and maritime pine, Norway and Sitka spruces, Douglas fir, poplar, and some noble hardwoods.

Genetic improvement of forest tree species is recent

Compared to other crop plants (cereals, vegetables, fruit trees), domestication of forest trees has started only recently: forestry breeding formally initiated in the USA in the 1950s then spread across European countries. So, except for some locally dysgenic exploitation of forests, introduction of exotic species and transfer of allochtonous populations (already frequent in the 1900s) which could hybridize with local populations, most forest tree species in Europe could still be considered as wild.

This is fortunate for forest tree breeders. Associated with a generally broad genetic variability, typical of most forest tree species in Europe, the absence of domestication of forest trees guarantees huge opportunities for genetic progress through selection. In addition, in parallel, it allows the organization of the conservation of gene pools. However, the recent interest in breeding forest trees also means that during the last few decades huge research efforts have been (and still are for some species) devoted to gaining basic knowledge on the biology of the species. Progress in breeding has been delayed accordingly.

A story in various steps

Huge efforts have been invested in studying the genetic variability of the main forestry species and their geographic organization. This has been an unavoidable preliminary step before breeding. With few exceptions, those studies started at an international level only in the 1940s with major conifers. They were strongly supported by IUFRO (International Union of Forest Research Organisations) and they largely benefited from the commitment of highly dedicated foresters and researchers, such as among others Prof. R. Schober for European larch, W. Langner for Japanese larch, A. Schwappach, W. Schmidt, S. Kociecki, M Giertych for Scots pine, O. Langlet, P. Krutsch and M. Giertych for Norway spruce, H. Barner and A. Fletcher for Douglas fir and Sitka spruce. For broadleaves (but also for some other conifers), studies have been more recent with initiatives supported by EU grants such as for ash (RAP project); for walnut (Walnut-Brain); for Douglas-fir (Forest, Eudirec); for Eurasian larch species (Sib larch) or by some national programmes (examples: ash, wild cherry).

Populations (natural and sometimes artificial ones) sampled over the whole natural range of the species (from a few tens to one thousand populations) were jointly planted and evaluated across many test sites (provenance trials) across Europe and sometimes beyond. Progressively, they delivered their results on the intra-specific genetic variability for adaptive, growth and architectural traits and at a later age for wood properties. They have been an incredible source of information for choosing the best-suited populations to begin breeding and for recommending populations to be deployed in forests prior to breeding and selection results.

In several countries and for some species, genetic improvement stops there. Based on these genetic variability results for adaptive and silvicultural traits, complemented or not with molecular or biochemical markers studies, regions of provenance have been delineated; seed stands have been selected and collection, transfer and deployment of seed sources have been organized. Regions of provenance correspond to geographic zones, ecologically uniform, with seed stands or seed sources presenting similar phenotypic or genetic characteristics. They are mainly defined for native species and it is a way of avoiding uncontrolled genetic pollution in local genetic material by seed sources collected outside the zone. However, regions of provenance are also defined for widely used exotic species.

Today, beyond their initial scope of genetic diversity studies, provenance trials also represent a temporary form of *ex situ* conservation; a reservoir for some extinct or endangered populations; an easy-access source of DNA material for genetic studies, etc. These trials and their related datasets accumulated over years are also revisited from the perspective of the threats of climate change to study the flexibility of populations to climate and the construction of reaction norms. Fifty years later, or even more for some species, many of these trials still exist but like many forest genetics field trials, they are in danger of being abandoned due to lack of funding and concern.

Based on this knowledge, plus trees (phenotypically superior trees in comparison to their neighbours) have been selected from the best suited populations either in the native range or in provenance trials and breeding populations have been established. Based on a few tens to several hundreds (sometimes thousands) of selected trees (clones), these populations are the core of further breeding and will evolve with breeding progress. Breeding cycles of recombination-testing-selection, aiming to increase the frequency of favourable genes for targeted traits, could then start. According to economic needs and local resources, short-term (usually one generation) or conversely long-term (several generations) breeding strategies have been engaged.

Short-term breeding strategies aim to release highly performing varieties, usually for a limited set of traits. The selection pressure (intensity) is commonly heavy and the genetic diversity of the released variety can be narrow (down to one cultivar up to a few individuals in mixture). Breeding is usually not planned beyond that first generation. The reduced genetic variability is indeed a major bottleneck for further genetic progress. In contrast, long-term breeding strategies are oriented to maintain a large enough genetic variability over time in the breeding population so as to allow genetic gains over breeding cycles. While building up genetic progress, genetic diversity is maintained and monitored through a careful organization of breeding populations, recombination of genotypes, selection process, and a clear separation of breeding and deployment populations.

Implicitly or not, breeding efforts are oriented towards improvement for given bio-geographic zones, sufficiently uniform from an ecological point of view for a given species. They are called ‘breeding zones’ (defined *a priori* on pedo-climatic criteria coupled or not with genetic data) or ‘deployment zones’ (defined *a posteriori*, based on performances of improved varieties) but this latter is probably more restrictive. Strong latitudinal gradients such as in Scandinavia or continentality gradients on the Continent or in the UK, for example, impose these organizational divisions. However, environmental conditions of these zones may be less homogeneous, in which case the stability of varieties over sites becomes a major selection criterion.

For forest tree breeding, time is a major constraint

Trees are long-perennial organisms with a commonly late sexual maturity. Obvious consequences are delays in recombination and in evaluation of genetic material: indeed, the optimal expression of some traits of interest (e.g. heartwood content, wood properties, resistance to some diseases) may be late and only observed in more mature material or after some extreme (often rare) climatic event. Therefore, strategies aim to shorten the breeding cycle span and to optimize genetic gains per unit of time. Progress in flower initiation and stimulation by mechanical means like stem girdling and/or chemical treatments such as injection of gibberellins have accelerated the recombination phase in several naturally late-reproducing species. Development of early indirect predictors (marker-assisted selection is one form of them) of traits targeted by selection in farm tests has enhanced efficiency (more gain per unit of time) of selection for several traits.

Selection is most commonly multi-traits

Overall whatever the species and the type of strategies, the same traits are targeted. Selection is most commonly multi-traits, which might impose some compromises between antagonistic traits. Most common traits of interest include: adaptation to abiotic (frost, drought, wind, etc.) and biotic (fungi, bacterial pathogens, insects, rodents) agents, growth, stem and crown form, branching, and wood properties (anatomical, physical, mechanical, chemical, biological and technological). Other traits can be added directly in relation to further deployment of varieties such as genetic stability of varieties over environments, ease of (sexual or asexual) mass propagation, etc. Selection criteria priorities or weights vary according to species and depend on the cultivation environment and industrial context.

Based on biological and genetic characteristics of the species, different breeding strategies have been developed taking advantage of species peculiarities such as inter-specific crossing possibilities and hybridization benefits (e.g. hybridization programmes for poplars and larches), selfing success to remove deleterious genes (e.g. in maritime pine to improve stem form), ease of generative (e.g. breeding programmes based on recurrent selection for Scots pine, Norway spruce and Douglas fir) or vegetative (e.g. clonal programme for wild cherry, partly for Sitka spruce) propagation, etc.

Release of improved varieties remains the final aim

Whatever the strategy used, selection and release of improved varieties remain the final aim. Forest tree varieties cover different forms: from *single individuals* (cultivar) propagated vegetatively (e.g. in poplars, wild cherry, chestnut), or *single half- or full-sib progenies* either vegetatively propagated (e.g. Sitka spruce) or produced in hybridization orchards (e.g. hybrid larch), to *synthetic varieties* produced in seed orchards (progenies usually from several tens of parent clones; e.g. Scots pine, Norway spruce, Douglas fir, wild cherry, ash, birch) or in hybridization seed orchards (e.g. hybrid larch).

Improvement of mass propagation techniques was another prerequisite to anchor breeding progress into forestry and a large amount of research work has been carried out in parallel to breeding. Again according to species characteristics, propagation can be envisaged either sexually or asexually. Seed orchards are the main way for generative production of varieties: they are special plantations of selected trees established so as to favour panmixia and managed to produce large and regular quantities of seed at a reasonable cost. Seed orchards are commonly used to produce varieties of pines, spruces, firs, larches but also several broadleaves (ash, cherry, birch, etc.). Vegetative propagation through cuttings is quite exclusively used for poplars and willows. It is also widely used now for Sitka spruce, wild cherry, etc. and it is attempted for several other species like hybrid larch, Douglas fir, and Norway spruce. Somatic embryogenesis in conjunction with cryoconservation is also an attractive alternative to cuttings for several species for which it is currently developed (pines, larch, Douglas fir).

With a strict regulatory framework at European level

Forest Reproductive Material is traded across Europe under four regulatory categories following OECD and EU (Directive 1999/105/CE) rules: ‘identified’ (yellow label), ‘selected’ (green label), ‘qualified’ (pink label) and ‘tested’ (blue label). The ‘identified’ category simply guarantees the origin of the material from a given region of provenance, but without any selection; the ‘selected’ category is represented by synthetic varieties collected in phenotypically selected seed stands; the ‘qualified’ category is represented by synthetic or hybrid varieties collected in seed orchards, the components of which have been selected for some criteria; the superiority of the variety is under evaluation. Finally, the ‘tested’ category corresponds to varieties the superiority of which has been demonstrated for some criteria in a given zone of deployment. They include seed stands, seed orchards, parents of family and cultivars.

Legal protection of forest tree varieties can also be obtained through Plant Variety Rights as long as the new varieties conform to DUS (Distinction-Uniformity-Stability) criteria. In forestry, it applies only to clonal material (cultivars) and it is thus restricted so far to poplars and willows, but cultivars from some other species like wild cherry, chestnut, or walnut, for which clonal propagation can be used, might also benefit from this protection.

A successful story

Breeding efforts, jointly developed with genetic research, have been intense during these last decades and have considerably improved our scientific knowledge in the biology, physiology, pathology and genetics of major forestry species as well as the technical expertise in field experimentation and assessment of various traits, sexual reproduction of species (control crosses, mass-production, seed handling), and vegetative propagation (cuttings, in vitro techniques).

Operationally these efforts have resulted in the selection and creation of improved varieties for nearly all forest tree species at the European level. Synthetic varieties from first-generation seed orchards are now commercialized in most countries for major conifers but also for some broadleaves. Second-generation or even third-generation seed orchards exist in some countries with most advanced breeding programmes of conifers like maritime pine in France or Scots pine in Scandinavia. Over 1,000 seed orchards covering more than 6,900 ha are currently available for nearly 40 different species in Europe. Clonal varieties of Sitka spruce obtained from elite families are also traded in some countries (e.g. UK, Ireland). Highly performing cultivars of several broadleaves (poplars, birch, willows, wild cherry, chestnut, black locust, alder, etc.) are also available for agro-forestry and forestry uses. In conclusion, improved varieties are now widely used in Europe in artificial plantations and they successfully contribute to the enhancement of wood production both in quantity and in quality and to the sustainability of forests.

But not without any threats … and new challenges

In several countries and for several species, benefits accumulated nowadays from improved varieties are very often the fruit of past breeding activities at a time when forest tree breeding was booming in Europe (1960–1990). It was not rare at that time to have breeding programmes for the same species ongoing in over 15–20 different research institutes (national and regional). From then on, cuts in budget and/or staff of breeding teams have dramatically depleted breeding efforts, bringing them close to extinction in some countries. As a consequence, greater synergy among breeding teams at national levels, reduction in the number of species bred for and concentration of efforts towards a limited set of species, re-orientation of research activities towards more cognitive genetic studies, or ongoing valorization of past efforts have been some of the options for breeders and their research institutes.

Meanwhile, climate change together with its trail of new biotic threats (pathogens and insects) severely question the adaptive potential of species and the sustainability of European forests in the long run. More urgently, foresters question the suitability of existing improved varieties to future climates, and especially of those selected 30–60 years ago in quite different climatic contexts. In addition, socio-economic needs continue to evolve with a constantly increasing need for wood, with renewed industrial demands (e.g. fuel wood, durable wood), and with higher societal pressures (as protection of biodiversity, forest amenity, environmental remediation). Meanwhile too, scientific progress in biotechnology in the broad sense, in mathematical modelling, etc. offers new possibilities for breeders, which have still hardly been integrated into breeding strategies.

Co-operation among european breeders is unavoidable and must be reinforced

It is clear that there are new threats and challenges at the European level; the native ranges of European species are wide and are not confined within national borders. The enlarged European Union has open new free spaces for trade of goods including Forest Reproductive Material with facilitated exchanges of seed and plants. Therefore the answers to new challenges can hardly be addressed by single national teams.

Attempts to foster forestry research across European teams and particularly research in forest genetics and breeding have been supported for at least two decades by the European Union through research projects (e.g. Gemini, Geniality, Walnut-Brain, Eudirec, Larch, RAP, Fraxigen) and through COST-projects (intergovernmental framework for European co-operation). A step forward has been achieved recently through the research infrastructure network TreeBreedex, again supported by the European Union. The aim of the TreeBreedex project is to network research teams and research infrastructures in forest tree breeding, scattered across the whole of Europe (28 institutes, 18 countries) and to foster co-operation among them.

Among achievements, several inventories of scientific and technical facilities have been produced; among these, the most significant is a fairly exhaustive inventory of forest tree genetic resources (populations, progenies, clones) and of experimental genetic trials for more than ten species, directly available through the TreeBreedex database. Frequent and regular occasions for exchange of information and expertise have been offered on scientific, technical, organizational and legal aspects linked to forest genetics and forest tree breeding. Some agreements, for example on common standards for assessment of traits in joined experimentation, have been reached. Among others, all these achievements reflect the will of European forest tree breeders to develop closer co-operation in genetic research and in breeding. The idea of a European Tree Breeding Centre has germinated and it must be worked out to make this network sustainable.

National or institutional forestry and research policies may impede such development but from a scientific and technical point of view, closer co-operation is needed for the reasons mentioned previously, in addition to erosion of staff and budget. Closer co-operation will require a courageous position of research and development institutes headquarters to bypass their own national or regional prerogatives and to convince their national forest policy authorities.

Meanwhile, European forest geneticists and breeders must progress in scientific and technical issues such as defining common breeding objectives, delineating transnational breeding zones, sharing experimentation protocols, developing new ones and agreeing on common standards, developing new breeding strategies, organizing concrete breeding workplans, etc. In parallel, breeding and research will need greater access to complementary facilities including genetic resources and field experimental trials to make progress in the ecology, biology and genetics of species.

The objective of this book

Knowledge of the current status of tree breeding, of major scientific results and achievements in terms of selection of Forest Reproductive Material in the different countries and research institutes was seen as a prerequisite for making progress in this way. It is thus natural that TreeBreedex partners have decided to collate this information in the form of a book. The objective was clearly to concentrate on breeding aspects (objectives, strategies, achievements and perspectives) for a set of species. Nine species or groups of species were retained based on the criteria that they are of broad interest throughout all European countries and are the object of genetic improvement, usually intensive. The initial aim was to include as well poplars for which active breeding is conducted across Europe but our position was finally that poplars – a more agricultural crop than a forest tree- would deserve by themselves a specific book. Maritime pine could have been a good candidate too to represent atlantic and Mediterranean forests but breeding experts for that species were not involved in the TreeBreedex project.

Breeding monographs have been written by sets of experts for each species. Each monograph aims to reflect the various breeding methods and achievements in European countries. Recommendations to authors were (1) to give a global overview instead of a detailed description by country and (2) to focus on biological specificities of forest species and to show how they have influenced the way breeding is conducted. In addition it was suggested to authors to report on the perspective of joint breeding.

We are thankful to J.C. Bastien, G. Douglas, F. Ducci, D. Krabel, S. Lee, V. Schneck, G. Jansson and J. Climent and to co-authors who have accepted the co-ordination of this difficult task to compile, digest, synthesize and release these monographs from information scattered around Europe and embedded in breeders' mind, in public and grey literature, in official or private documentation. We also acknowledge the contribution of all partners of the TreeBreedex project who have accepted to dig out this information and to share it.

Finally, we are very grateful to Ruth Noble (Freelance Editor) who thoroughly and patiently reviewed and edited the text.

TreeBreedex partners

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Part I
Breeding of Conifers

Chapter 2
Larches (*Larix* sp.)

Luc E. Pâques, Elena Foffová, Berthold Heinze, Marie-Anne Lelu-Walter, Mirko Liesebach, and Gwenael Philippe

2.1 Introduction

2.1.1 Species and Distribution

Larch (*Larix sp.*) is one of the most abundant conifers in the northern hemisphere where it can be found both at high latitudes and at high elevations. It comprises around ten species distributed over the three continents, North America, Europe and Asia.

Larix decidua is the only native species in Europe. European larch is phylogenetically related to *Cedrus* (genus *Pinaceae* with short shoots). It occurs naturally

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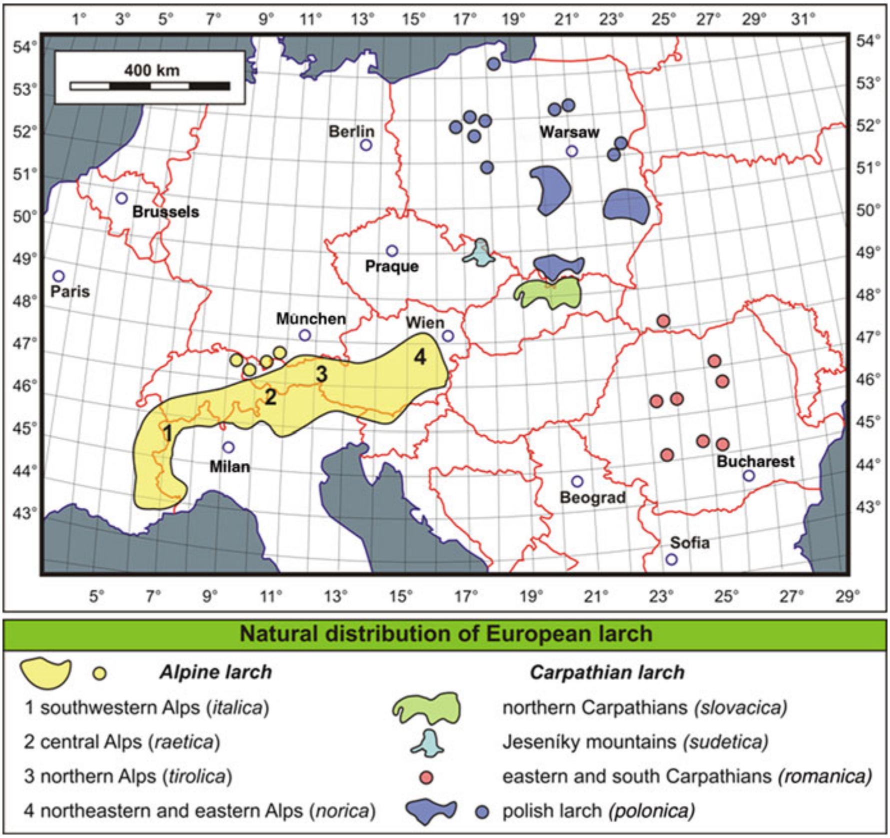

Fig. 2.1 Schematic map of the natural range of European larch (*Larix decidua* MILL.) based on Schütt et al. (2002), Blattný and Šťastný (1959), Šindelář (1999) and Chylarecki (2007)

mainly in the mountainous ranges in the Alps, the Sudeten Mountains (Jeseníky Mountains) – at the border between the Czech Republic and Poland – and in the Western Carpathians (North Slovakia and adjacent hilly areas in Southeastern Poland). Some residual stands are also present in Central Poland and in the Romanian Carpathians (Fig. 2.1). Its post-glacial migration was stopped westwards at the French and Italian Alps and it never reached the Pyrénées. Native stands are mainly located at high elevations (1,000–2,900 m) up to the timber line in the western Alps but some exceptions exist in the eastern part of the Alps in Austria and in Central Poland where larch occurs naturally down to 150 m (Fig. 2.2).

Compared to other major native conifers in Europe such as Norway spruce or Scots pine, the native range of European larch is scattered and small. It is estimated that it slightly exceeds 600,000 ha with a major presence in the Alps (over 85 %).

Nevertheless, the cultivated area of larch has been widely extended by foresters firstly within its native range due to traditional farming lands being abandoned as in the Alps (both downwards and upwards) but also well beyond it towards northern and western Europe (Fig. 2.3). Originally, European larch was used but several other

Fig. 2.2 European Larch in the Alps. Larch is one of the rare deciduous conifers. Its amenity value is highly appreciated in forest landscaping (Photo: INRA – L.E.Pâques)

Fig. 2.3 Fast growing Hybrid Larch in Belgium (20 year-old) (Source: DMF – DEMNA – 2008)

Table 2.1 Larch native and cultivated area (in ha) across Europe and total coniferous forest area

	Larix			All conifers	
Country	Native range	Cultivated range	Total	Total	% total conifers
Austria	~110,000	Not known	155,000	3,371,000	4.6
Belgium	0	10,169	10,169	226,441	4.5
Czech Rep.	8,500	85,000	93,500	1,933,341	4.8
Denmark	0	19,258	19,258	288,072	6.7
Finland	0	15,000	15,000	17,500,000	<1
France	26,369	93,640	120,009	4,470,000	2.7
Germany	25,000	272,400	297,400	6,084,400	4.9
Great Britain	0	130,000	130,000		
Ireland	0	22,960	22,960	462,580	5.0
Italy	289,926	92,447	382,372	1,651,153	23.2
Lithuania	0	781	781	1,151,900	<1
Netherlands	0	17,900	17,900	196,000	9.1
Poland	48,690	97,380	146,070	6,784,000	2.2
Romania	4,500	12,500	17,000	1,920,000	<1
Slovak Rep.	19,900	26,500	46,400	783,500	5.9
Sweden	0	?	?	22,652,000	–
Ukraine	0	5,000 (35,000)[a]	5,000		
Switzerland[b]	71,500	?	71,500	726,100	9.8
Slovenia	3,161 (14,000)[a]	–	3,161 (14,000)[a]	1,184,104 (total forest)	–
Total	**607,546**	**900,935**	**1,553,480**		

[a]Area where larch is present but is not the major species
[b]WSL, Inventaire forestier national suisse, 10.03.2010

Larix species have also been used. Indeed, in more oceanic sites where summer droughts are rare (the western Massif Central in France, Belgium, the British Isles, Denmark, etc.), Japanese larch (*L. kaempferi*), a native of Hondo Island, has usually been preferred to European larch. In addition, in Scandinavia, *L. sibirica* or some of its hybrids which are more resistant to cold, have been successfully introduced. In north-western Europe, the inter-specific hybrid between *L. decidua* and *L. kaempferi* (*L.* × *eurolepis*) is also planted today.

Altogether, it is estimated that artificial plantations of larch outside the native range of *L. decidua* contribute to some additional 900,000 ha. Therefore altogether, larch covers around 1.5–1.6 million ha which is small when compared to other commercial conifers (Table 2.1). Indeed, it is estimated that larch forest represents around 4 % of the total coniferous forest area in Europe, and less than 1 % of total forests.

It is currently impossible to obtain figures relating to timber production of larch because in many countries larch wood is sold mixed in with other red wood like Douglas fir or Scots pine. If we consider an average wood production of 3 m^3/ha/year in mountainous ranges and 12 m^3/ha/year in the lowlands, the total timber production across Europe would probably not exceed 12 million cubic metres per

Fig. 2.4 Heartwood is always abundant in larch trees; it is the most valuable part of timber in particular when natural durability and/or aesthetics are needed (*upper disk*: 40 year-old Hybrid Larch from Wales; *lower disk*: 230 year-old European Larch from French Alps) (Photo: INRA – L.E.Pâques)

year. As a consequence, its economic interest appears to be mainly regional, as in mountainous zones where it plays a major role in the local economy and the maintenance of rural populations.

2.1.2 Benefits and Uses of Larch

Among many advantages, larch is particularly appreciated by foresters for its fast juvenile growth, its soil frugality and its overall good stem architecture. It is also wind, snow, fire and air-pollution resistant (Olaczek 1986). Among temperate conifers, it has one of the best wood qualities in terms of wood density, mechanical properties (strength), natural durability and aesthetics. Compared to other coniferous species in Europe like Scots pine or Douglas fir, its reddish heartwood, the most valuable part in terms of durability, is formed very early and it is already abundant in young trees (Pâques 2001) (Fig. 2.4). Its wood can be used in many different contexts from flooring or wall panelling to outdoor structures like bridges. Due to its changing foliage colour over the seasons, its amenity value for forest landscaping is also esteemed.

Pests in larch are rare: the most nocive are: larch canker due to *Lachnellula willkommii* (Hartig.) Dennis, an Ascomycetes which can be found in sites with high atmospheric humidity, mainly in Central Europe but also in the Alps, and *Meria laricis* Vuill., which affects needles (yellowing and cast) and is seen more and more frequently due to warmer, more humid springs. Among insects, *Zeiraphera diniana* Gn is the most harmful but it is largely limited to the Alps with widespread defoliation occurring at regular intervals. Defoliation can also be caused by larvae of the common sawfly *Pristiphora laricis* Hartig (*Hymenoptera*, family *Tenthredinidae*). An important pest in cultures and seed orchards is the Western Larch Case-Bearer *Coleophora laricella* Hübner (*Lepidoptera*, family *Coleophoridae*). The caterpillars of the species destroy the larch needles by burrowing. When abundant, the aphids (*Adelges laricis* Vall. and *Sacchiphanthes viridis* Ratz.) can also affect vitality.

Larch is used in many different silvicultural situations both for afforestation and reforestation, in pure or mixed stands such as currently seen with beech in Central Europe. It has been widely planted in the Alps on steep slopes for soil protection and to combat avalanches. It is used as a nursing species on windy sites before the introduction of more delicate species, for reforestation in heavily polluted areas (e.g. the Ore Mountains), but also for afforestation of abandoned farmland and in agro-forestry, for the enrichment of forests.

2.1.3 Breeding Origins

The widespread introduction of larch to the lowlands of Western Europe at the beginning of the twentieth century was followed a few decades later by the collapse of plantations due in particular to the use of maladapted populations from the Alps resulting in frost damages and canker. In the second part of the twentieth century, Japanese larch was used instead but it failed in more continental sites where there was the risk of summer droughts.

These failures were the origin of the tree breeding programmes in Europe: they raised the need to scientifically assess genetic diversity at population level and to evaluate their interest for reforestation outside the native range of European larch. Although some population testing work started even earlier, IUFRO international trials (series 1940/44 and 1956/58) were key milestones in larch breeding. In parallel, the discovery at the beginning of the twentieth century of the inter-specific hybrid between European and Japanese larches in Scotland (Dunkeld) first (Henry and Flood 1919), and later on in Belgium (Delevoy 1949) and elsewhere in Europe led to increased interest in hybrids.

While in many countries exotic species planting has increased dramatically (e.g. Sitka spruce in the British Isles, Douglas fir in France), surprisingly larch planting has remained on a relatively small scale despite its many advantages. There are probably several reasons for this, such as the lack of stem straightness in comparison with commonly used Norway spruce and Douglas fir, the higher sensitivity to wild game, etc. However, a particularly important reason is related to its biology, and more specifically to its problematic low aptitude for propagation, both sexually and asexually. This seriously impedes both breeding (active recombination over breeding cycles) and mass-production of improved varieties for deployment. This becomes even more critical when dealing with inter-specific hybridization: this will be explained later.

2.2 The Starting Point: Description of the Geographical Organization of Genetic Diversity

The first introductions of European larch in plantations outside its native range failed because of inappropriate choice of the right seed source. Seed from Alpine stands was commonly used for practical reasons associated with the availability of seed. The material failed mainly because of an inadequate phenology resulting in frost damage combined with or caused by larch canker due to *Lachnellula willkommii*.

This was suspected early on but it became obvious only when results from comparative provenance trials brought up definite proof.

2.2.1 Geographical Variability of European and Japanese Larches

Despite its small and scattered native range, European larch occupies ecologically contrasting sites (in terms of climate and soil) which has led to many different ecotypes. Classically, three main sources are recognized, namely the Alpine larch, the Sudeten larch (often called '*sudetica*') and the Carpathian larch (often called '*polonica*'). Some discrete morphological features differentiate them but above all they are physiologically and phenologically different.

2.2.1.1 Brief Description of European Larch Ecotypes (by E. Foffova)

European and Siberian larches have a common origin; larch reached Europe from Siberia in the same way as the Swiss pine, which occupies similar natural sites (Šiman 1953). In the Pleistocene glacials, larch survived in the area between the Alpine and continental ice sheets – in the Carpathians and adjacent southern regions, as well as on territory that is now part of Russia. During moderate interstadials, larch disseminated to larger areas in Europe as recorded by evidence not only from the Alps and the Carpathians but also from lower situated sites on territories of France, Poland and Hungary (Szafer 1913; Vorel 1979). In the warmer postglacial period, this more or less conjunct area was reduced to isolated areas in the Alps, Carpathians and Jeseníky mountains (Sudetes) with sites where this cold tolerant species with high need for light was able to meet competition of the spruce, beech and fir (Opravil 1980; Vorel 1979).

The disjunctive distribution with variable growing conditions in the late Quarternary period caused morphological, biochemical and physiological differentiation of the European larch. As the main features for taxonomic distinction of European larch (Domin 1930; Rubner and Svoboda 1944), cone size and number or shape of scales were taken into account, although they also showed high variability within the observed populations (Hrubý 1933; Bałut 1969).

Authors dealing with larch (Raciborski 1890; Cieslar 1904; Wóycicki 1912; Szafer 1913; Domin 1930; Rubner and Svoboda 1944; Šiman 1943, 1953; Svoboda 1953; Dumitriu-Tataranu et al. 1970) also attempted to describe the ecologically different larch populations according to morphological features. Variable taxonomic evaluation of characteristics resulted in the diverse nomenclatorial concepts of the species with description of numerous taxa (small species or subspecies and varieties), most of which are disregarded by present botanical nomenclature.

Evaluating various morphological traits (cone length, winged seed length and full seed weight) and physiological traits (dry twig mass, time and speed of shooting and content of terpens, growth speed in juveniles) in provenances from the whole native area of European larch confirmed the clinal character of geographical variability of the larch. Populations originating from the most distant sites (from the south-western Alps on one side and from East Poland on the other side) show the biggest differences in the studied biometric traits (Rubner and Svoboda 1944; Šindelář 1966; Bałut 1969). According to Šindelář (1966), this geographical variability supports the division of the species *Larix decidua* Mill. into two main groups: Alpine larch and Carpathian larch (including Sudeten, Slovak, Polish and Romanian larches). Some authors (Šiman 1943; Svoboda 1953; Dumitriu-Tataranu et al. 1970) described these groups as subspecies with further division into varieties and climatypes.

The taxonomic classification of the European larch used by these authors is compared in Table 2.2.

According to the current botanical approach (Franco 1964; Jasičová 1966; Boratynski 1986; Skalická and Skalický 1988), the species *Larix decidua* Mill. is divided into two subspecies, defined in different ways:

Larix decidua Mill. subsp. *decidua*
Larix decidua Mill. subsp. *polonica* (Racib.) Dom.

The name *Polish larch* is used only for larches with small cones and concave scales from Poland and Ukraine. In such concept, the provenances from Jeseníky, Slovakia and Roumania belong to the nominate subspecies.

Jasičová (1966) states that the larches growing in Slovakia belong mainly to the *Larix decidua* Mill. subsp. *decidua* with transitive forms belonging to *Larix decidua* subsp. *polonica* (Racib.) Dom. In the same way Skalická and Skalický

Table 2.2 Comparison of the taxonomic classification of European larch

	Alpine larch	Carpathian larch
Šiman (1953)	*L. decidua* Mill. subsp. *alpica* Šim. with varieties: *raetica* (Central Alps), *tirolica* (N Alps), *italica* (SW, S Alps) *norica* (NE, E Alps)	*L. decidua* Mill. subsp. *carpatica* Šim. with varieties: *slovacica* *With climatypes:* *tatrensis (High Tatra),* *subtatrensis (Low Tatra),* *šarišiensis (NE Slovakia),* *polonica* *sudetica* *romanica*
Svoboda (1953)	*Larix europea alpica* (Šim.) Svob. with varieties: *raetica* *tirolica* *italica* *norica*	*Larix europea carpatica* (Dom.) Svob. with varieties: *silesiaca* (Sudeten) *tatrensis* (Slovakia) *polonica* *romanica*
Dumitriu-Tataranu et al. (1970)	*Larix decidua* subsp. *decidua*	*Larix decidua* subsp. *polonica* (Racib.) Dom. with varieties: *polonica* *carpatica* (Carpathians, Sudeten)

(1988) assigned the larch growing in the Czech Republic to the *Larix decidua* subsp. *decidua*. Nevertheless they do not exclude the presence of autochthonous *Larix decidua* Mill. subsp. *polonica* (Racib.) Dom. in the Jeseníky Mountains before the widespread introduction of Alpine larch into Czech forests in the eighteenth and nineteenth centuries and recognize the virgin character of some populations in the Czech Republic. On the other hand, Münch (1933) explained that the introduction of Alpine larch populations mainly failed (through low growing potential and susceptibility to canker). According to Šindelář (1966), the excellent allochthonous provenances of larch growing outside the Sudeten natural range (Hrotovice, Adamov, Paršovice, Křivoklát, White Carpathians) are very probably (and some proven by archived documentation) derived from Sudeten larch.

In forestry practice, failures observed after the introduction of larch onto sites outside the natural distribution range of the species manifested the strong need to know the origin of the reproductive material used and to describe the ecological characteristics and adaptability of basic material (Münch 1933; Šiman 1943). To avoid ambiguous taxonomical nomenclature for describing the geographical variability, foresters (Šindelář 1999; Schober 1985; Laffers 1988; Vidaković 1991; Chylarecki 2007) now prefer to divide the native distribution area of European larch into geographical regions or to group the regional populations in a way comparable with Šiman's (1953) species concept.

Alpine Larch

The Alps represent the largest compact area in Europe where larch occurs naturally – they extend from the Maritime Alps in the south-west of France through Switzerland and Italy to north-west Yugoslavia to the Vienna wood (Wienerwald) in north-eastern Austria. There larches grow on a broad vertical range between 300 m (Eastern Alps) to 2,400–2,900 m a.s.l. (south-western Alps) mostly in mixed stands associated with *Picea abies*, *Abies alba*, *Pinus sylvestris*, *Pinus cembra*, *Pinus mugo* and *Fagus sylvatica*. Favourable conditions for the species are in regions with cold continental climate and rainfall above 1,000 mm – especially in the Central Alps. Generally the Alpine larches, especially those from high elevations, have a lower growing potential than the larches from Carpathian region. They are characterized by bigger ovate cones with length varying between 15 and 44 mm, and with visible bracts and slightly curved scales numbering around 16–81 scales per cone (Rubner and Svoboda 1944; Šindelář 1966). Larches from the south-western Alpine border and high elevations tend to have female flowers which are mainly red and their seeds are markedly bigger and heavier than those from the eastern part of the natural range of the species. Alpine larch is also characterized by higher dry mass content in the twigs (Šindelář 1967).

Due to variable growing conditions in the Alpine area and noticeable differences in the regional Alpine larch populations, it is common to further divide the area into four sub-regions:

1. Southern Alps including Maritime Alps (Italian larch). On the southern edge of the Alps in southern France and Italy (Maritime, Cottian, Graian, Lepontine, Vizentine Alps) larch grows in the warm continental mountainous climate at a range of 300 to 2,400–2,500 m a.s.l., the optimum being between 1,000 and 1,600 m a.s.l. The provenances from this region grow slowly, stem form is often poor and crowns are broad.
2. Central Alps (Raetic larch). The highest closed part of the Alps with the cold continental mountain climate is represented by the southern cantons Wallis, Tessin and Graubünden in Switzerland and by the central part of Tyrol, Carinthia and Western Styria. The altitudinal range covers the alpine (1,700–1,800 m a.s.l.), subalpine (1,200–1,700 m a.s.l.) and montane (under 1,200 m a.s.l.) zones. In high altitudes the growing conditions are harsh, e.g. the vegetation period in Oberengadin is very short (2–3 months). In such conditions above the spruce zone the larch grows in large sparsely pure stands with admixture of *Pinus cembra* (larch meadows).
3. Northern Alps (Tyrolian larch). The area on the northern calcareous border of the Alps from Vorarlberg, Algäu, Northern Tyrolia to the Salzburger Alps and Berchtesgaden has a mountainous climate with maritime influence. The larch occurs here mainly in altitudes between 1,000 and 1,600 m a.s.l. in the mountain-subalpine zone. The growing performance is variable, but these larches are generally not suitable for transfer to the lowlands as used to be done in previous centuries.

4. North-eastern and eastern borders of the Alps (Nordic larch). The region on the eastern border of the Alps is influenced by the warm continental climate and covers the territories of the Wienerwald, Semmering, Oetscher and lower mountains in Lower Austria and Western Styria at altitudes from 250 to 800 m a.s.l. These colline and submontane larches have the best trunk form (straight) and best growth potential among the Alpine larches. They are both geographically and morphologically closer to the Sudeten larches (Tschermak 1935).

Carpathian Group

The other parts of the natural distribution area of the European larch are separated from the Alps by the broad band of the Donau Valley, where the species does not occur. In comparison to the Alpine larch the larch from the Carpathian region grows faster. The stem quality is variable, but generally the provenances from the higher altitudes (High Tatra) are much better than the lowland provenance – especially of some Polish origins, e.g. Chełmowa Góra (Šindelář 1999). The Carpathian larches have smaller globulous cones measuring 10–25 mm in length with invisible bracts, straight or concave scales numbering around 11–70 per cone and smaller seeds than Alpine ones.

This area is split into three smaller regions and in isolated remnant stands in the Romanian Carpathians:

1. *Jeseníky mountains* (*Sudeten or Silesian larch*)
   The original distribution of the authochthonous Sudeten larch is represented by a small part of the North Moravian–Silesian region which covers the mountains of Lower Jeseník and eastern slopes of Hrubý Jeseník with a small disjunct occurrence at Ruda and Moravou (Fig. 2.5). Most of the area lies within the Czech Republic, only its northern part penetrates slightly onto Polish territory (forest units Prudnik, Pokrzywna, Dębowiec, Glubczyce), where the old stands with native Sudeten larches are maintained (Chylarecki 2007). Sudeten larch grows mainly in altitudes from 300 to 800 m a.s.l. on the sites, where competition from fir, beech and spruce is reduced. In higher altitudes it is replaced by spruce. In contrast to Alpine larches from high elevations, the demands of colline ecotypes (both Sudeten and Polish) for light are lower and they are able to grow in the shade of other tree species to a limited extent (Šiman 1953).

   Sudeten larch grows in a temperate climate, somewhere between oceanic and continental and also between lowland and mountainous climates. The average annual temperatures range between 5.8 and 8.5 °C, the annual rainfall between 600 and 1,000 mm.

   The Sudeten larch is known for its good productive ability in different ecological conditions, and has been successfully introduced on various sites in European countries. There are also numerous allochthonous provenances which are fairly certain to be of Sudeten origin growing in the Czech Republik, Slovakia, Germany and Poland; these are known for their good adaptability as well as

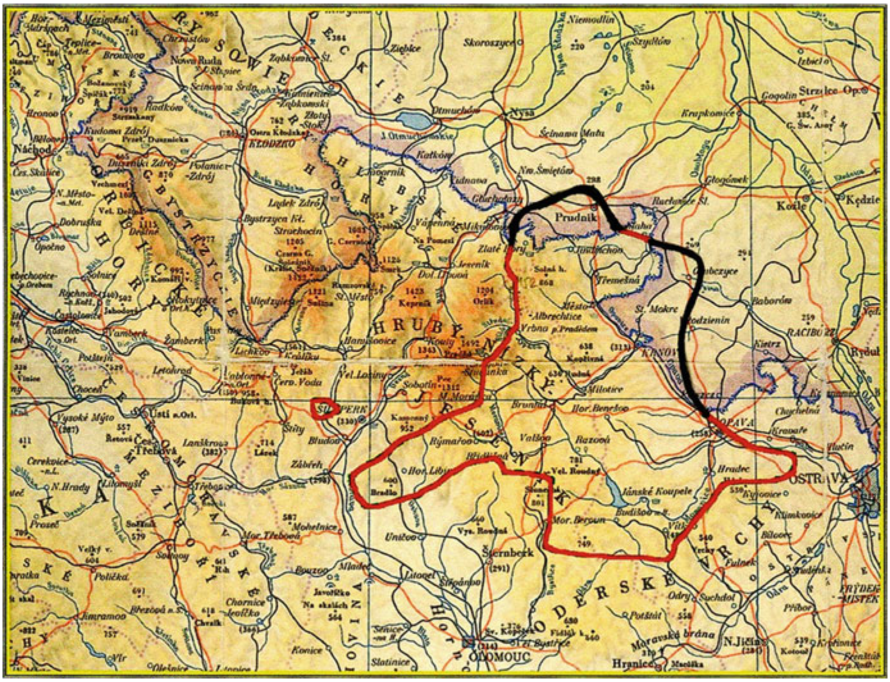

Fig. 2.5 Area of Sudeten ecotype of European larch, between the Czech Republic and Poland, according to Rubner (1943), Šindelář (1999) and Chylarecki (2007)

excellent production and are used as the basis for acquiring reproductive forest material. The total reduced surface of the native Sudeten larch is only about 9,000 ha.

2. *Polish larch*
   The Polish larch is another lowland ecotype characterised by a fast growth, but a worse stem straightness. Naturally the Polish larch is mainly concentrated in the Świętokrzyskie Mts. (Góry Świętokrzyskie), in the region of Małopolska upland (Wyżyna Małopolska). Its is also noticed in the adjacent Lubelska upland (Wyżyna Lubelska), Roztocze upland (Roztocze) and in the mountains at the Polish-Slovakian border (Beskidy Zachodnie Mts., Tatra Mts. and Pieniny Mts.). Scattered remnant stands of the Polish larch can be found to the north from this area in the Rawska upland (Wysoczyzna Rawska, Grójec and Rawa Mazowiecka) and in the Dobrzyńska upland (Wysoczyzna Dobrzyńska, Konstancjewo forest unit). Larch grows there in the submontane and colline zones from 150 to 600 m (Chylarecki 2000). The natural distribution area of the Polish larch is characterized by a temperate continental climate (Šindelář 1999).

   Allochthonous stands of Polish larch originating mainly from the Świętokrzyskie Mountains can be found outside its natural range in other regions of south-eastern and north-eastern Poland and in Lithuania (Chylarecki 2007).

3. *Western Carpathians* (*Slovak or Tatra larch*)
   In the Western Carpathians, larch covers a compact area in the northern and north-eastern part of Slovakia. Both the highest Slovakian mountain ranges (High and Low Tatra, Fatra and the northern part of the Slovak Ore Mountains – Slovenské Rudohorie) as well as the submontane region of Spiš, represent the native range.

   This area is divided into three different parts which correspond to the provenance regions defined for European larch in Slovakia:

– High Tatra (Vysoké Tatry): larch grows there in conditions comparable with the central Alps mainly on granite, in mixed stands with spruce, at elevations from 800 to 1,500 m, and together with *Pinus cembra* it reaches the tree line at altitudes up to 1,600 m.
– Central Mountains – Nízke Tatry (Low Tatra), Malá and Velká Fatra (Fatra), Spišsko-gemerský kras (Carst region at the eastern border of Low Tatra) and the northern part of the Slovenské Rudohorie (Slovak Ore Mountains). Larch grows here at altitudes between 400 and 1,200 (1,400) m mixed with spruce, fir and beech. It is common on carbonate rocks as remnant stands with *Pinus sylvestris* – also in lower altitudes, because on such sites the competition ability of climax species is reduced.
– North-eastern Slovakia – larch occurs naturally in the mountains of Levočské vrchy and Spišská Magura at altitudes between 400 and 900 m, either in mixed stands or in larch meadows around the settlements of Uloža, Nižné, Vyšné Repaše and BrezoviČka, established for specific agricultural use as in the Alps, but at much lower elevations. Larch also grows further to the east (Sabinov and Prešov regions), but was probably introduced there (Štastný 1971).

4. *Eastern/southern Carpathians – Romanian larch*
   The natural range of larch in the southern and eastern Carpathians is disjointed, represented by a total area of 4,500 ha in 5 isolated centres: Ceahlău, Ciucaş, Bucegi, Lotru and Apuseni. Romanian larch generally grows in micropopulations on abrupt rocks, conglomerates, limestone, or detritus with Swiss pine and Norway spruce at altitudes over 1,200 m (even up to 2,050 m in the Bucegi Mountains). Only in the Apuseni Mountains does it descend into more moderate altitudes of between 600 and 1,200 m.

   The seed weight and cone size of Romanian larch are between those of Alpine larch and Sudeten larch. It differs from ssp. *polonica* by its mountainous and subalpine habitat and it is different from ssp. *decidua* as it has smaller cones. It is an ecotype of altitude similar to the larch from the Tatra Mountains. Autochthonous Romanian larch enters the growing season early, has a straight trunk, branches of average thickness and is not attacked by canker.

2.2.1.2 Geographic Variability of European Larch

Two major sources of information on the geographic variability of European larch are available: one from the two international IUFRO series of provenance