Global Ecology and Biogeography Letters (1998) **7**, 181–188

RESEARCH LETTER

Palaeoecological, biogeographical and palaeoclimatological implications of early Holocene immigration of *Larix sibirica* Ledeb. into the Scandes Mountains, Sweden

LEIF KULLMAN *Department of Physical Geography, Umeå University, S-901 87 Umeå, Sweden*

Abstract. For the first time, Holocene macroremains (cones and wood) of *Larix sibirica* Ledeb., radiocarbon dated between 8700 and 7500 BP, have been recovered from two sites in the Scandes Mountains of Sweden. The sites are separated by >300 km and lie in the present subalpine and low alpine belts, respectively. Existing pollen-stratigraphical records have not suggested the presence of *Larix* in the Holocene beyond its present range, i.e. >1000 km to the east in Russia. Hence, the pollen analytical method should be used more cautiously when inferring subcontinental-continental biogeographical dynamics. It appears that *Larix* immigrated rapidly by long-distance jump dispersal soon after the deglaciation. The same pattern has emerged for *Picea abies* (L.) Karst. and some thermophilous broadleaved tree species. This might be a more general mechanism for tree spread during the early Holocene. Step-wise migration and migrational lags could be quite unimportant elements within tree palaeobiogeography. This increases the prospects for interpretation of long-term and large-scale changes in plant cover performance in terms of expansion/decline relative to climatic change. Today, *Larix sibirica* prospers in continental climates with extremely cold winters, thus it is reasonable to infer that early-Holocene winters in western Fennoscandia could have been similar to, or slightly colder than those of today. This contention conflicts with previously published simulations using General Circulation Models, pollen-climate response surfaces and other retrospective devices, which suggest a strongly oceanic climate with winters >2°C warmer than present.

Key words. Holocene palaeoecology, plant immigration, *Larix sibirica*, macroremains, palaeoclimatology, subalpine vegetation, Sweden.

INTRODUCTION

Objective, high-quality presence-absence data are critical to the interpretation of Holocene continental and sub-continental biogeographical patterns, both in terms of climatic change and intrinsic vegetation dynamics. Inferences of tree migrational histories at different spatial scales since the latest glacial termination have relied mainly on pollen-stratigraphic records (Davis, 1976; Huntley & Birks, 1983; Webb, 1988; Birks, 1989). A current research project conducted in the Scandes Mountains of Sweden, based on extensive and systematic search and analysis of tree macroremains, has highlighted the inability of pollen analysis to reveal and date accurately the immigration of some tree species into a specific region or site. For instance, well-established, frequently cited descriptions of *Picea abies* (L.) Karst. as a typical late-Holocene immigrant have been altered, with major implications for the comprehension of general post-glacial plant spreading history and for palaeoclimate reconstruction (Kullman, 1995a, 1996a). Continued research within this project has, for the first time, documented Holocene macrofossils (cones and wood) of *Larix sibirica* Ledeb. (Siberian larch) at two widely separated sites in the subalpine/alpine regions of the Scandes Mountains in Sweden, 8700–7500 BP. Previously, the palaeohistory of *Larix sibirica* in Fennoscandia and western Russia during the present interglacial was virtually unknown, although *Larix* was assumed never to have occurred west of its present range limit, i.e. 1000–1200 km east of the study region (Huntley & Birks, 1983; Lang, 1994; Donner, 1995). Here, the details of these fundamentally new findings are reported together with a tentative discussion of some methodological, palaeobiogeographical and palaeoclimatological aspects.

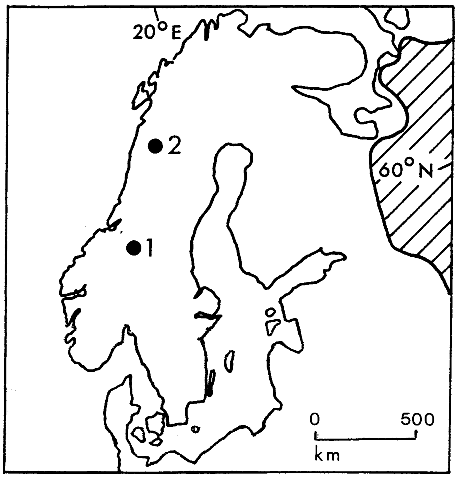

Fig. 1. Location of the investigated sites (1 and 2). The hatched area shows the western fringe of the present range of *Larix sibirica* Ledeb.

STUDY SITES

Site 1, in the province of Jämtland (Fig. 1), is on the E-facing flank (910 m a.s.l.) of Mt. Sylarna (63° 02′N, 12° 20′E). The climate has a local-maritime character. The terrain is gently sloping and dominated by hummocky moraine (relative heights <10 m) with minor pools and mires filling the depressions. Deglaciation took place about 9100 yr BP or somewhat earlier (Lundqvist, 1986). On dry ground, the plant cover is dwarf-shrub heath, while mires occupy most depressions, with *Eriophorum angustifolium* Honck as a characteristic species. The landscape is open, wind-swept and locally snow-poor in the winter.

The site is *c*. 10 m above the local tree-limit (i.e. trees >2m high) of mountain birch (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman). The nearest living mature pines (*Pinus sylvestris* L.) grow 20 km to the north, *c*. 680 m a.s.l. More detailed data concerning the regional and local climate, geomorphology, Quaternary vegetation development and present vegetation are provided by Lundqvist (1969) and Kullman (1995b).

Site 2, Krabbfjällnäset (520 m a.s.l.), is situated at the NNW shore of a small point of land in Lake Överuman, province of Västerbotten (66° 07′N, 14° 37′E) (Fig. 1). For most of the time since a hydroelectric reservoir was established in the mid-1960s, these remains have been drowned and the peat matrix has gradually eroded. The water-level was exceptionally low during the spring and early summer of 1996, which enabled the findings reported here.

The terrain is flat and mainly covered with mires interspersed with birch groves (Ericaceae in the understory). The area was deglaciated around 9000 BP (Lundqvist, 1986). The climate is local-maritime and the exposed character of the site leads to a sparse snow cover and permafrost mounds, such as a few minor palsas. The site is located *c*. 280 m below the local tree-limit (>2 m tall trees) of birch and just 10 m or so above the potential pine tree-limit (Kullman, 1991). Scattered spruce trees occur in the subalpine birch belt to slightly above 600 m a.s.l. The local physiography, climate, vegetation and Quaternary history were outlined by Ulfstedt (1976) and Kullman (1991, 1992, 1993).

METHODS

In connection with extensive and systematic surveys of subfossil wood deposits in general, the macrofossil remains described here were sampled at the surface of eroded peat accumulations. Cones of *Larix sibirica* Ledeb. were positively identified on the basis of their shape, the number of scales and their surface structure (cf. Tutin *et al*., 1964; Edlund, 1966) and confirmed by inspection by prominent Swedish dendrologists, Dr Annika Hofgaard and Mr Sören Källgren. Species identification of subfossil wood was conducted by Dr Thomas Bartholin, who has developed a method to distinguish wood of *Larix* from *Picea*, based on the structure of the bordered pits in the ray tracheids (cf. Bartholin, 1979). Radiocarbon dating was carried out by Beta Analytic Inc., Miami, Florida. Dates are reported as uncalibrated ^{14}C yr BP (=AD 1950), with a half life of 5568 ± 30 years. They have been corrected for deviations in δ^{13}C.

AUTECOLOGY OF LARIX SIBIRICA

Larix sibirica is a shade-intolerant and deciduous conifer, which is a major constituent of the forest tundra and arctic tree-line in northern Russia (Hustich, 1966; Nikolov & Helmisaari, 1992). With increasing climatic continentality eastwards from Fennoscandia, *Larix sibirica* becomes an increasingly important component of the light taiga and forest tundra, growing in mixed stands with *Pinus sylvestris, Picea abies* and *Betula* spp. This species is competitive in strongly continental and seasonal climates with short, warm and dry summers. Its western range limit towards Fennoscandia is fairly diffuse and assumed to be set effectively by climatic oceanicity influenced by the White Sea (Oksanen, 1995). More than most other trees, *Larix sibirica* endures long and extremely cold winters, often growing on permafrost (Sakai & Larcher, 1987; Nikolov & Helmisaari, 1992), and is relatively little prone to winter desiccation (Gower & Richards, 1990).

Optimal growth conditions are met on nutrient-rich, well-drained and aerated soils. In general, *Larix* avoids waterlogged situations and successful regeneration necessitates bare mineral soil (Edlund, 1966; Nikolov & Helmisaari, 1992). The lightweight seeds are easily spread by wind over great distances (von Berg, 1910; Srutek & Leps, 1994). The longevity of *Larix sibirica*, which is relatively fire-tolerant, exceeds 350 years (Nikolov & Helmisaari, 1992).

RESULTS

Macrofossils of *Larix* were recovered at two sites, separated by *c.* 360 km, in the low-alpine/subalpine belts of the Scandes Mountains in Sweden (Fig. 1). The mixed and resorted character of the focused peat deposits excluded any local pollen stratigraphical studies.

Site 1 (Mt. Sylarna, Jämtland)

Subfossils of *Larix sibirica, Pinus sylvestris* and *Picea abies* were retrieved from the exposed peat face of a recently eroded mire at the fringe of a small water-filled depression (Fig. 2). Wood and cones of *Pinus sylvestris* occurred in quite large quantities, although only one specimen was dated, since many samples of *Pinus* from this specific elevation have been dated previously, yielding ages between 9000 and 7000 BP (Kullman, 1995b). The radiocarbon dates are presented in Table 1. The most notable feature is the dating of *Larix* at *c.* 8700 BP (cones), while the dates of *Pinus* (wood) and *Picea* (cone) are well within the range of previous dates (Kullman, 1995b, 1996a).

Site 2 (Krabbfjällnäset, Västerbotten)

An accumulation of subfossil tree remains occurred 5–10 m outside the scarp (0.5–1 m high) of a wave-eroded peat bog. The recorded species were *Larix sibirica* (Fig. 3), *Pinus sylvestris* (predominant), *Picea abies*, and *Betula pubescens*. Several subfossils of *Pinus* and *Betula* from the vicinity of this site have been dated previously, ranging between 8700 and 2700 BP and 6900 and 4000 BP, respectively (Kullman, 1992, 1993). The subfossils (both cones and wood) lay on the surface of a thin layer (0.1–0.3 m) of peat or mud, which was the residue of a previous 1–2 m deep peat accumulation. Dating results are given in Table 2. *Larix sibirica* was present here *c.* 8300–7500 BP, concurrent with *Pinus* and *Betula*.

DISCUSSION

Methodological considerations

Larix sibirica grew and reproduced in western Fennoscandia, within the elevational range of the present-day subalpine birch belt, for at least a millennium (8700–7500 BP), far outside its present-day geographical range. Previous pollen stratigraphical studies carried out in this region have not provided any indications of Holocene presence of this species in northern Sweden (Lundqvist, 1969; Huntley & Birks, 1983; Berglund *et al.*, 1996). The nearest well-dated regional pollen diagram to any of the sites is at Hemavan, *c.* 37 km SE of site 2 (Engelmark, 1996) and shows no *Larix* pollen. The first arrival of *Picea* has been inferred from this diagram to be *c.* 2000 BP. That is *c.* 5500 yr later than the date recorded here by macroremains. This compares well with results from the southern Scandes (the same region as Site 1), showing similar early arrival of *Picea* and some deciduous and thermophilous tree species (*Alnus glutinosa* (L.) Gaertn., *Betula pendula* Roth and *Tilia cordata* Mill., without palynological detection (Kullman, 1996a, 1998). Thus, substantial discrepancies between pollen and macrofossil records are by no mean exceptions and are particularly understandable in the case of *Larix*, with its relatively weak pollen production and poor dispersal of easily corroded pollen (Lang, 1994). Thus, an implication of the present findings concerns the use of pollen data for palaeobiogeographical analyses of key events. As demonstrated also in some previous studies (e.g. Bush & Hall, 1987; Peteet 1991), pollen analysis alone may be an ambiguous tool for accurate range-limit reconstructions and associated climate correlations (cf. Bennett, 1988; Birks, 1993; Lang, 1994; Kullman, 1995a, 1996a). In the latter context, it is crucial to determine whether distribution of plants are in

Fig. 2. Site 1 has the character of an eroded peat deposit, where subfossil cones of *Larix sibirica* Ledeb. were retrieved from the surface.

Table 1. Radiocarbon dates for Sites 1 and 2, in the Scandes Mountains, Sweden.

Lab number	^{14}C age (yr BP)	Species	Material
Site 1 (Mt. Sylarna, Jämtland)			
Beta-96582	8700 ± 90	*Larix sibirica*	Cone
Beta-99191	8010 ± 60	*Pinus sylvestris*	Wood
Beta-99403	5310 ± 50	*Picea abies*	Cone
Site 2 (Krabbfjällnäset, Västerbotten)			
Beta-96586	8270 ± 70	*Larix sibirica*	Cone
Beta-99414	7550 ± 60	*Larix sibirica*	Wood
Beta-96580	8240 ± 60	*Pinus sylvestris*	Wood
Beta-99201	7410 ± 90	*Picea abies*	Wood
Beta-96579	4750 ± 70	*Picea abies*	Wood
Beta-96581	8190 ± 90	*Betula pubescens*	Wood

equilibrium with climate. That issue can only be judged securely if the timing of the local arrival is well-established and migrational lags can be excluded. Thus, macrofossil analysis stands out as an obligate complement to pollen records (cf. Berglund *et al.*, 1996; Penalba & Payette, 1997). Reasonably, certain published tree migrational histories could benefit from some re-evaluation in the light of the results presented here. The argument often raised, based on coleopteran subfossil remains, that the time of arrival of trees may substantially lag behind climate change (Coope, 1977; Pennington, 1986), might at least in part emerge as an artefact, related to the prevalence of the palynological method within studies of vegetation history.

Fig. 3. The subfossil cones of *Larix sibirica* Ledeb. recovered at Site 2.

Palaeobiogeographical implications

Despite limited knowledge about the exact position in the east of the late-glacial range-limit of *Larix sibirica*, it is now plausible that after deglaciation it rapidly invaded western Fennoscandia, perhaps with big jumps. In that respect, the results agree with new megafossil evidence of the immigration history of *Picea abies* into the same region (Kullman, 1995a, 1996a), where it was reported that *Picea* occurred more than 5000 yr earlier than had been inferred from pollen analyses. That is shortly after the deglaciation and it leaves little time for a protracted, directional and generation by generation migrational history. At present the ecological processes behind the rapid Holocene tree spreading are poorly understood. Well-established observations have shown, however, that seeds in general may spread several hundreds of kilometres, in particular over frozen surfaces or in higher atmospheric layers (cf. Ridley, 1930; Pielou, 1979). Interestingly, Ritchie & MacDonald (1986) inferred equally rapid N–S spread of *Picea glauca* ([Moench] Voss) during the early Holocene in western North America.

Although we have no factual basis for going beyond the tree species discussed here, it is tempting to speculate that the immigration of North European trees was not generally limited by their migratory speed or the position of their late-glacial refugia. Thus, expressing the immigration process of trees (inferred from pollen data) in terms of meters per year (e.g. Davis, 1983; Huntley & Birks, 1983) may be a misleading abstraction with some taxa. The data on *Larix* reported here are more consistent with inferences that many plant species invaded early and rapidly during the Holocene by long-distance dispersal from distant refugia without step-wise sequential migration (cf. Huntley, 1994). It is easy to agree with Birks (1989) that early-Holocene spreading is an enigmatic but fundamental aspect of biogeographic change and structuring in need of intensive study.

The past frequency and abundance of *Larix* in the landscape can only be tentatively hypothesized. It appears unlikely that the two sites reported here were the only ones along the entire Scandes. After the present findings were made, however, many sites with abundant macroremains of different tree species (cf. Kullman, 1992; 1995b) have been selectively scrutinized for the presence of *Larix*, without positive evidence, thereby suggesting that *Larix* never attained a full-ranged distribution. Presumably, a sparse pattern of minor outliers was established along the Scandes Mountains, far west of the main distributional area. In these woodlands, *Pinus sylvestris* was the dominant tree species and *Betula pubescens* and *Picea abies* occurred as subordinate constituents in the landscape (Kullman, 1995b; 1996a). That situation resembles the one currently prevailing at the western frontier of *Larix sibirica* in the taiga and the forest tundra of northern Russia (cf. Nikolov & Helmisaari, 1992).

The occurrence of *Larix* has a bearing on an old phytogeographical problem in northern Fennoscandia (Nordhagen, 1933; Dahlskog, 1980). Today, a small group of plant species, including *Athyrium crenatum* (Somerf.) Rupr., *Clematis sibirica* (L.) Mill., and *Cystopteris sudetic*a A. Br. et Milde., with their main distribution far in the east, roughly coinciding with the current range of *Larix sibirica*, grows at a few scattered outlying localities in Fennoscandia, usually with a strongly continental local climate. Up to the present day, however, no factual clues to their Holocene histories (pollen or macrofossils) have been presented. In view of the discovery of the early-Holocene appearance of *Larix sibirica*, with similar climatic affinity, followed by its subsequent disappearance, it may be hypothesized that these species were also early eastern immigrants. Subsequently, they may have decreased in frequency in response to an increasingly oceanic type of climate and have survived as relicts only within the most continental local climates.

Palaeoclimatic inferences

The extent of the time interval bracketed by the *Larix* dates from the two widely separated parts of the Scandes suggests that *Larix* both established and regenerated for several generations. The *Larix* remains from the two sites alone provide no clue as to whether the youngest date of 7500 BP represents the true temporal limit of *Larix*. That date, however, broadly coincides with the initiation of a discrete subalpine birch forest belt, a process deduced to reflect gradually increased climatic oceanicity, decreased seasonality, and a deeper and more stable snow cover (Kullman, 1995b). In response to the same course of climatic development, *Picea abies* became an increasingly dominant tree species in the landscape of northern Sweden during the late Holocene (cf. Tallantire, 1977; Kullman, 1996a, b). Thus, *Larix sibirica* and *Picea abies*, which immigrated at roughly the same time, have performed individualistically and contrarily in relation to continually decreasing continentality, as summers became cooler and more humid. These subsequent processes would mainly have concerned variations in dominance, i.e. phases of population expansion or decline, which is what can be inferred by pollen analysis (cf. Birks, 1989; Kullman, 1996a, b).

Considering the specific climatic demands and tolerances of *Larix sibirica* (see above), one may tentatively make some climatic inferences for the early Holocene, *c.* 9000–7500 BP. The occurrence of *Larix* fits well with the theoretical model of a strongly seasonal climate, with warm and dry summers during that period, in response ultimately to orbital forcing of insolation (COHMAP Members, 1988). Such a situation is supported for this region by earlier megafossil evidence of an elevational pine tree-limit maximum in the early Holocene and a contemporary modest role and relatively low tree-limits of mesomorphic tree species such as *Picea abies, Betula pubescens* and *Alnus incana* (Kullman, 1995b, 1996a).

Prior to the present finds of *Larix sibirica*, few proxy indicators of the early-Holocene winter climate in the Scandes Mountains were available. Glacier data (lake sediments) exist (e.g. Snowball & Sandgren, 1996), but are not unequivocally interpretable in terms of winter temperature. The current cryophytic and strongly continental ecological tolerances of *Larix sibirica* might imply a markedly different early-Holocene climate than the oceanic conditions advocated by General Circulation Models and pollen-climate transfer surfaces, which have suggested that that the early-Holocene winters were >2°C warmer than at present (Harrison, Prentice & Bartlein, 1992; Huntley & Prentice, 1993). The present data also conflict with a reconstruction based on glacier equilibrium-line altitudes and tree-limits, which claims that early-Holocene winters in the southern Scandes were relatively mild and snow-rich (Dahl & Nesje, 1996). On the other hand, severely cold and snow-poor winters, as envisaged by the Milankovitch insolation anomaly (e.g. Wigley & Kelly, 1990), do not comply with the documented spruce palaeohistory. Monitoring of growth and vigour during the past few decades in conjunction with dendroclimatological and age structure analyses demonstrate that spruce is very sensitive to low winter soil temperatures (a function of both ambient air temperature and snow depth) and would probably not have survived winter temperatures below those prevailing during the Little Ice Age (Kullman, 1995a, 1996b; Kullman & Engelmark, 1997). In particular, since shallower snow-depths than today have been inferred for that period (Huntley, 1988; Kullman, 1995b), it might be reasonable to suggest that early-Holocene winters were similar to, or only slightly colder than, those of today. Some additional support for the contention that the presence of *Larix* does not necessarily indicate extremely low winter temperatures might lie in the fact that *Larix sibirica*, planted (1930s) in the subalpine birch forest, *c.* 35 km SE of Site 2, grows well and has overtopped the native birches (Kullman, 1980). However, it is important to stress that biogeographical deductions from artificial range extensions may be of limited value (cf. Prentice, 1983).

Alternative to a climatic explanation, the lack of finds of *Larix* from the mid- and late-Holocene might relate to anthropogenic disturbance. Sparse and climatically marginal Fennoscandian *Larix* trees, which may have grown on the best soils and also offered wood of the required qualities (e.g. resistant to rot), would have been easily exterminated by man, as discussed by Hemberg (1899) for the western outliers of *Larix sibirica* in Russia. In particular, Site 2 is within a region that has been extensively used by man since at least 7000 BP (Holm, 1991).

ACKNOWLEDGMENTS

Financial support was provided by the Swedish Natural Science Research Council. I thank Chris Caseldine, Lena Kjällgren and Serge Payette, who critically read an earlier draft of this paper.

REFERENCES

Bartholin, T. (1979) The *Picea-Larix* problem. *IAWA Bull.* **1979**, 7–10.

Bennett, K.D. (1988) Holocene geographic spread and population expansion of *Fagus* in Ontario, Canada. *J. Ecol.* **76**, 547–557.

Berg, F. von (1910) Gehölzarten der sibirischen Ostküste. *Mitteil. Deutsch. Dendrolog. Gesell.* **1910**, 215–226.

Berglund, B.E., Barnekow, L., Hammarlund, D., Sandgren, P. and Snowball, I. (1996) Holocene forest dynamics and climate changes in the Abisko area, northern Sweden. *Ecol. Bull.* **45**, 15–30.

Birks, H.H. (1993) The importance of plant macrofossils in late-glacial climatic reconstructions: an example from western Norway. *Quat. Sci. Rev.* **12**, 719–726.

Birks, H.J.B. (1989) Holocene isochrone maps and patterns of tree-spreading in the British Isles. *J. Biogeogr.* **16**, 503–540.

Bush, M.B. & Hall, A.R. (1987) Flandrian *Alnus*: expansion or immigration? *J. Biogeogr.* **14**, 479–481.

COHMAP Members (1988) Climatic changes of the last 18000 years: observations and model simulations. *Science,* **241**, 1043–1052.

Coope, G.R. (1977) Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Phil. Trans. R. Soc. Lond., Ser. B,* **280**, 313–337.

Dahl, S.O. & Nesje, A. (1996) A new approach to calculating Holocene winter precipitation by combining glacier equilibrium-line altitudes and pine tree-limits: a case study from Hardangerjøkulen, central southern Norway. *The Holocene*, **6**, 381–398.

Dahlskog, S. (1980) The Siberian fern *Athyrium crenatum* (Somf.) Rupr. found in Sweden at Kvikkjokk, SW Lule Lappmark. *Acta Phytogeogr. Suec.* **68**, 51–60.

Davis, M.B. (1976) Pleistocene biogeography of temperate deciduous forests. *Geoscience and Man* **13**, 13–26.

Davis, M.B. (1983) Quaternary history of deciduous forests of eastern North America and Europe. *Ann. Mo. Bot. Grdns.* **70**, 550–563.

Donner, J. (1995) *The Quaternary history of Scandinavia,* 200 pp. Cambridge University Press, Cambridge.

Edlund, E. (1966) Den sibiriska lärken i Norrland och Dalarna som skogsträd och industriråvara. *Sveriges Skogsvårds. Tidskr.* **64**, 461–550 (in Swedish).

Engelmark, R. (1996) North Sweden. *Palaeoecological events during the last 15 000 years: regional syntheses and palaeoecological studies of lakes and mires in Europe* (ed. by B.E. Berglund, H.J.B. Birks, M. Ralska-Jasiewiczowa and H.E. Wright), pp. 266–510. John Wiley, New York.

Gower, S.T. & Richards, J.H. (1990) Larches: deciduous conifers in an evergreen world. *BioScience,* **40**, 818–826.

Harrison, S.P., Prentice, I.C. & Bartlein, P.J. (1992) Influence of insolation and glaciation on atmospheric circulation in the North Atlantic sector: implications of general circulation model experiments for the Late Quaternary climatology of Europe. *Quat. Sci. Rev.* **11**, 283–289.

Hemberg, E. (1899) Sibiriska lärkträdet. *Tidskr. för Skogshushåll.* **27**, 83–106 (in Swedish).

Holm, L. (1991) The use of stone and hunting of reindeer. *Archaeol. Environ.* **12**, 1-141.

Huntley, B. (1988) Glacial and Holocene vegetation history: Europe. *Vegetation history* (ed. by B. Huntley and T. Webb III), pp. 341–383. Kluwer Academic, Dordrecht.

Huntley, B. (1994) Late-Devensian and Holocene palaeoecology and palaeoenvironments of the Marone Birkwoods, Aberdeenshire, Scotland. *J. Quat. Sci.* **9**, 311–336.

Huntley, B., and Birks, H.J.B. (1983) *An atlas of past and present pollen maps for Europe: 0-13000 BP,* 667 pp. Cambridge University Press, Cambridge.

Huntley, B. & Prentice, I.C. (1993) Holocene vegetation and climates of Europe. *Global climates since the last glacial maximum* (ed. by H.E. Wright, Jr., J.E. Kutzbach, T. Webb, III, W.F. Ruddiman, F.A. Street-Perrott and P.J. Bartlein), pp. 136–168. University of Minnesota Press, Minneapolis.

Hustich, I. (1966) On the forest-tundra and the northern tree-lines. *Rep. Kevo Subarct. Res. Stat.* **3**, 7–47.

Kullman, L. (1980) Trädslagsfördelning i nutid och sen historisk tid i översta Umeälvsdalen *Sveriges Skogsvårds. Tidskr.* **78**, 52–75 (in Swedish with English summary).

Kullman, L. (1991) Pattern and process of present tree-limits in the Tärna region, southern Swedish Lapland. *Fennia,* **169**, 25–38.

Kullman, L. (1992) Orbital forcing and tree-limit history:

hypothesis and preliminary interpretation of evidence from Swedish Lappland. *The Holocene,* **2**, 131–137.

Kullman, L. (1993) Holocene thermal trend inferred from tree-limit history in the Scandes Mountains. *Global. Ecol. Biogeogr. Letts,* **2**, 24–31.

Kullman, L. (1995a) New and firm evidence for Mid-Holocene appearance of *Picea abies* in the Scandes Mountains, Sweden. *J. Ecol.* **83**, 439–447.

Kullman, L. (1995b) Holocene tree-limit and climate history from the Scandes Mountains, Sweden. *Ecology,* **76**, 2490–2502.

Kullman, L. (1996a) Norway spruce present in the Scandes Mountains, Sweden at 8000 BP: new light on Holocene tree spread. *Global Ecol. Biogeogr. Letts,* **5**, 94–101.

Kullman, L. (1996b) Rise and demise of cold-climate *Picea abies* forest in Sweden. *New Phytol.* **134**, 243–256.

Kullman, L. & Engelmark, O. (1997) Neoglacial climate control of subarctic *Picea abies* stand dynamics and range limit in northern Sweden. *Arct. Alp. Res.* **29**, 315–326.

Kullman, L. (1998). The occurrence of thermophilous trees in the Scandes Mountains during the early Holocene: evidence for a diverse tree flora from macroscopic remains. *J. Ecol.* **86**, 421–428.

Lang, G. (1994) *Quartäre Vegetationsgeschichte Europas*, 462 pp. Gustav Fischer Verlag, Stuttgart.

Lundqvist, J. (1969) Beskrivning till jordartskarta över Jämtlands län. *Sver. Geol. Unders.Ser. Ca,* **45**, 1–418 (Swedish with English summary).

Lundqvist, J. (1986) Late Weichselian glaciation and deglaciation in Scandinavia. *Quat. Sci. Rev.* **5**, 269–292.

Nikolov, N. & H. Helmisaari (1992) Silvics of the circumpolar boreal forest tree species. *A systems analysis of the global boreal forest* (ed. by H.H. Shugart, R. Leemans and G.B. Bonan), pp. 13–84. Cambridge University Press, Cambridge.

Nordhagen, R. (1933) De senkvartaere klimavekslinger i Nordeuropa og deras betydning for kulturforskningen. *Instituttet for Sammenlignende Kulturforskning Serie A,* **XII**, 1–246.

Oksanen, L.(1995) Isolated occurrences of spruce, *Picea abies*, in northernmost Fennoscandia in relation to the enigma of continental mountain birch forests. *Acta Bot. Fenn.* **153**, 81–92.

Penalba, M.C. & Payette, S. (1997) Late-Holocene expansion of eastern larch (*Larix laricina* [Du Roi] K. Koch) in northwestern Québec. *Quat. Res.* **48**, 114–121.

Pennington, W.A. (1986) Lags in adjustment of vegetation to climate caused by the pace of soil development: Evidence from Britain. *Vegetatio,* **67**, 105–118.

Peteet, D.M. (1991) Postglacial migration history of lodgepole pine near Yakutat, Alaska. *Can. J. Bot.* **69**, 786–796.

Pielou, E.C. (1979) *Biogeography,* 351 pp. John Wiley, Chichester.

Prentice, I.C. (1983) Postglacial climatic change: vegetation dynamics and the pollen record. *Progr. Phys. Geogr.* **7**, 273–286.

Ridley, H.N. (1930) *The dispersal of plants throughout the world*, 744 pp. Reeve, Ashford.

Ritchie, J.C. & MacDonald, G.M. (1986) The pattern of post-glacial spread of white spruce. *J. Biogeogr.* **13**, 527–540.

Sakai, A., &. Larcher, W. (1987) *Frost survival of plants*, 321 pp. Springer-Verlag, Berlin, Germany.

Snowball, I. & Sandgren, P. (1996) Lake sediment studies of Holocene glacial activity in the Kårsa valley, northern Sweden: contrasts in interpretation. *The Holocene,* **6**, 367–372.

Srutek, M. & Leps, J. (1994) Variation in structure of *Larix olgensis* along the altitudinal gradient on Paektu-san, Changbai-shan, North Korea. *Arct. Alp. Res.* **26**, 166–173.

Tallantire, P.A. (1977) A further contribution to the problem of the spread of spruce (*Picea abies* (L.) Karst.) in Fennoscandia. *J. Biogeogr.* **4**, 219–227.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D., Walters, S.M. and Webb, D.A. (1964) *Flora Europaea*, Vol. 1, 464 pp. Cambridge University Press, Cambridge.

Ulfstedt, A.-C. (1976) Geomorphological maps 25E and 25F Umfors. *Statens Naturvårdsverk PM*, **731**, 1–86.

Webb, T. III 1988. Glacial and Holocene vegetation history: Eastern North America. *Vegetation history* (ed. by B. Huntley and T. Webb III), pp. 385–414. Kluwer Academic, Dordrecht.

Wigley, T.M.L. & Kelly, P.M. (1990) Holocene climatic change, ^{14}C wiggles and variations in solar irradiance. *Phil. Trans. R. Soc. Lond. A,* **330**, 547–560.