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Source: Arctic, Antarctic, and Alpine Research, 40(1) : 104-110

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(06-120)[KULLMAN]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 40, No. 1, 2008, pp. 104–110

Thermophilic Tree Species Reinvade Subalpine Sweden—Early Responses to Anomalous Late Holocene Climate Warming

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Abstract

Consistent with general predictions and earlier empirical studies, it appears that recent climate warming has started to affect large-scale biogeographical patterns in northern Sweden. Long-term, systematic monitoring in permanent altitudinal belt transects reveals spread of broadleaved thermophilic tree species with quite different life histories into the subalpine forest belt. Saplings of *Quercus robur, Ulmus glabra, Acer platanoides*, *Alnus glutinosa*, and *Betula pendula* have responded to altered climatic conditions by jump-dispersal in the order of 50–300 km northwards and 500–800 m upwards. Thereby, they have reinvaded elevations where they grew during the warmest phase of the Holocene, 9500–8000 years ago, but were subsequently extirpated by Neoglacial cooling. Confined to the past 15 years or so, these unique observations are consistent with background climatic data, i.e. warming of all seasons. The results contribute to more realistic vegetation models by stressing that at least certain plant species are able to track climate warming without substantial migration lag.

DOI: 10.1657/1523-0430(06-120)[KULLMAN]2.0.CO;2

Introduction

One of the most important tasks for contemporary vegetation ecology is to document plant cover changes over the past 100 years, with the ultimate purpose of projective modeling. During this interval, climate change and various human impacts are assumed to have turned the Earth system into an unprecedented stage, which is expected to prevail if mainstream climate change scenarios (IPCC, 2001a) are borne out (Pickard, 2002; Crutzen, 2002).

The recent warming phase, most distinct over the past few decades, has affected ecosystems and species in widely different parts of the world (Grabherr et al., 1994; McCarty, 2001; Parmesan and Yohe, 2003; Penuelas and Boada, 2003; Root et al., 2003; Kullman, 2004a; Walther et al., 2005). High mountains at high latitudes play a key role in early detection of ecological responses to the current climate transformation. This is due to relatively large anticipated temperature changes here and since many resident species exist at the limits of their climatic tolerance (IPCC, 2001b).

In northern Sweden, warming by 1.2 °C since the early 20th century and up to the present has evoked upshifts of altitudinal (alpine) tree lines by a maximum of 200 m, to a position unsurpassed during the past 7000 years or so (Kullman and Kjällgren, 2006). In addition, substantial upward migration of ground cover species, i.e. herbs, sedges, grasses, ferns, and dwarf shrubs, by an average of 200 m implies increased plant species richness on high alpine mountain summits (Kullman, 2007a). In line with this progressive warming-driven transformation of the subalpine/alpine landscape, it has been predicted that thermophilic woody species, e.g. of the genera *Quercus*, *Ulmus*, and *Corylus*, are likely to shift northwards into the high-latitude boreal forests of Norway and Sweden, given that the current warming trend remains (Boer et al., 1990; Holten and Carey, 1992). With this background, I here report the anomalous phenomenon of recent migration of broadleaved thermophilic tree species from distant low-lying sources into the subalpine belt of south-central Sweden.

Study Area

This study is located in the southern Swedish Scandes (province of Jämtland), just east of the main divide in a transition zone between oceanic and continental climates. The nearest meteorological weather station (Storlien/Visjövalen, 642 m a.s.l. and 20 km to the northwest) provides data for the period 1961–1990. The mean temperatures for January, July, and the year are −7.6, 10.7, and 1.1 °C, respectively. Mean annual precipitation is about 900 mm. The highest mountain peaks range between 1300 and 1800 m a.s.l. and foothills 700–800 m a.s.l.

A subalpine belt and upper tree line (minimum tree height of 2 m) with predominant mountain birch (*Betula pubescens* ssp. *tortuosa*) prevails in the region. Solitary specimens of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) occur regularly in the lower reaches of the birch belt. The tree lines of *Betula*, *Picea*, and *Pinus* are positioned approximately 950, 850, and 800 m a.s.l., but with great local variation depending on site and aspect. Impact of past land-use on tree line positions is negligible.

Methodological Approach

The urgent need for real-world data, based on long-term systematic observations at the same locations, is increasingly stressed if we are to understand and predict responses of species and communities to altered climatic conditions. In particular, a realistic comprehension of plant migration rates are essential for the generation and testing of projective vegetation models (cf. Holten and Carey, 1992).

The present study relies on intentional search for thermophilic broadleaved deciduous trees within a regional network of sites intended for long-term standardized monitoring in the southern Swedish Scandes (Kullman, 2001). Contained herein are baseline data on tree lines and vegetation since the early 20th century. More than 200 elevational transects across the tree line

TABLE 1

Location and size of all specimens of thermophilic tree species encountered in the subalpine forest belt.

Species	Locality	Altitude (m a.s.l.)	Coordinates	Height (m)
Acer platanoides	Åreskutan	905	63°24.732′N; 13°04.689′E	0.3
Acer platanoides	Storsnasen	632	63°14.946′N; 12°25.653′E	0.3
Acer platanoides	Enafors	530	63°16.670′N; 12°21.436′E	0.4
Acer platanoides	Tandövala	770	60°50.186′N; 13°10.479′E	0.2
Acer platanoides	Alsberget	710	64°39.896′N; 17°35.891′E	0.3
Alnus glutinosa	Storsnasen	705	63°12.290′N; 12°23.682′E	0.3
Alnus glutinosa	Handöl	530	63°15.410′N; 12°26.677′E	1.3
Betula pendula	Storsnasen	680	63°13.845′N; 12°25.477′E	1.1
Betula pendula	Tandövala	770	60°50.195′N; 13°10.498′E	0.5
Betula pendula	Städjan	1020	61°54.940′N; 12°52.845′E	0.4
Betula pendula	Städjan	935	61°54.585′N; 12°53.082′E	0.3
Quercus robur	Predikstolen	1055	62°52.758′N; 12°24.099′E	0.2
Ulmus glabra	Åreskutan	970	63°24.751′N; 13°04.675′E	0.4
Ulmus glabra	Laptentjakke	990	63°08.348′N; 12°25.551′E	0.2

ecotone and with a width of 200 m are systematically spaced over an 8000 km^2 area. These are scrutinized intermittently for shifts of tree line positions and broad-scale vegetation/floristic changes, e.g. invasion of alien plant species. The high value of this area for the purpose of monitoring local elevational displacements and immigration processes is further enhanced by a thorough and documentary regional study of the altitudinal limits of all vascular plants in the early 1950s (Kilander, 1955). In addition to recordings from this network, some casual observations from outside localities are reported. These mainly concern the regional distribution and northern tree lines of this group of species, with particular focus on *Quercus robur*. From a biogeographical point of view, there is a special interest devoted to the northern distribution limit of *Quercus robur*. This is the most important and distinct boundary (*Limes Norrlandicus*) below the alpine tree line. It separates the boreonemoral zone, with predominantly warmth-demanding taxa, from the boreal zone where cold-tolerant species prevail (Sjörs, 1999).

Precise locations and altitude (m a.s.l.) are obtained with a GPS navigator. Geographical coordinates are given in degrees latitude and longitude.

Results

RECORDS IN PERMANENT TRANSECTS

During the most recent survey of the monitoring transects, 2003–2005, saplings of some thermophilic broadleaved species have been recorded. *Quercus robur, Ulmus glabra, Acer platanoides*, and *Alnus glutinosa* have their main distribution area in the nemoral and boreonemoral zones of southern and mid-Sweden/Norway and at elevations many hundred meters below those of the new colonists discovered in this study. *Betula pendula* grows closer to the high mountains and is less thermally demanding than the other species, although it is the most thermophilic birch species in Fennoscandia. Previously, it was unknown in the mountain taiga (Kullman, 2005). None of these species have been recorded during prior surveys of the concerned transects, the most recent one in 1988.

All five species of this warmth-demanding group have been uncovered during the past few years at extremely high elevations, well outside their previous natural ranges and biogeographical zones. Table 1 accounts for these records and their appearance. Documentary photographs are given as Figures 1 and 2.

All recovered specimens are of low stature and judged to be less than 10 years of age. There is nothing in their growth habitus, e.g. multiple stems, to suggest that they have been growing at their sites for lengthy periods as tiny suppressed individuals. Except for *Quercus*, they appeared in seemingly undisturbed ground cover. In the case of *Quercus*, two specimens were found close together in a spot physically disturbed by reindeer trampling. In all cases, surrounding vegetation was mainly of mesic and meadow-like character.

In particular, the highest stations for *Quercus, Ulmus*, and *Acer* are confined to thermally favorable S-SW–facing slopes with relictual forest floor vegetation and species remaining from the warmest phase of the Holocene (cf. Smith, 1957; Kilander, 1955).

Indications of substantially improved climatic preconditions for tree growth in the concerned transects are provided by evidence of large upshifts (100–170 m) of the birch tree lines at these specific localities since the early 20th century (Kullman, 1979 updated).

A WIDER CONTEXT

Relative to the nearest natural sites for tree growth existing today, i.e. the empirical limits, the new stations accounted for here are located 500–800 m higher and 50–300 km distant (Fig. 3). However, the exact positions of the potential (climatic) limits of tree-sized and reproducing individuals of the species here concerned are likely to be positioned at higher elevations. Possibly, the empirical limits have been pushed downwards and southwards by extensive and selective logging and pasturing during past centuries (Andersson and Birger, 1912; Aas, 1970; Huldén, 2001). This may explain why sown or planted individuals in parks and gardens often thrive far to the north of the empirical limit. For example, *Quercus robur* grows in the form of large trees as high as 300 and 500 m a.s.l. in interior parts of northern Sweden. Initially, many of these specimens owe their existence to plantation trials in the warm 1930s and have subsequently expanded in size during the past few warmer decades, when they have also attained reproductive maturity. In many cases, they have started to produce offspring in wide circles (5–30 km) off their sites, often in natural or semi-natural vegetation (Johansson, 2000). In fact, saplings are occasionally naturalizing over the entire area between the empirical (northern) limit and the new and extended sapling limit now reported from the high mountains. Until the late 1990s, the northernmost occurrence of spontaneous cultural escapes of oak were close to the Bothnian coast, at 63°17′N, 12°44′E, 30 m a.s.l. (Johansson, 2000). In this region, *Quercus* has reproduced abundantly during the past decade, and

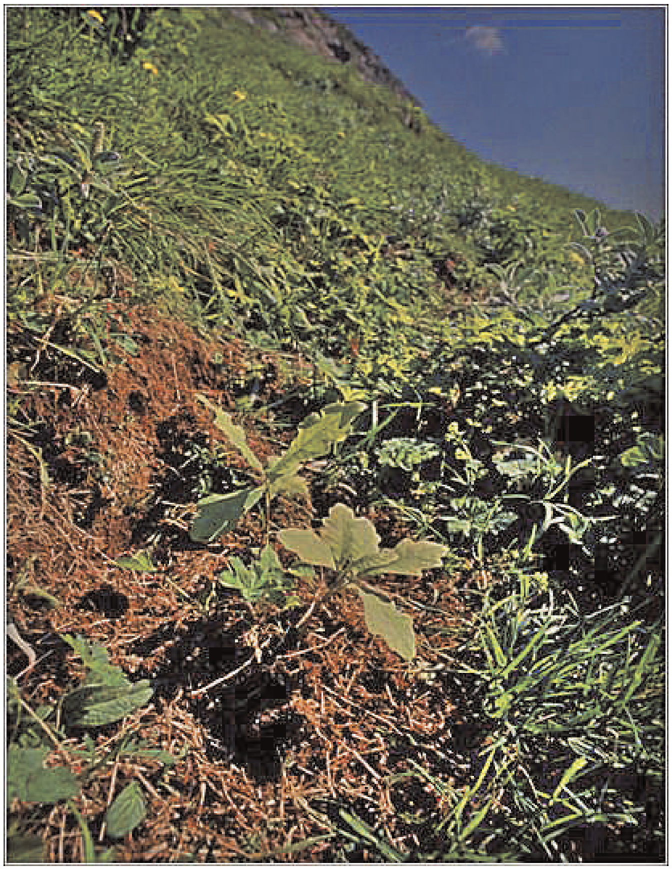

FIGURE 1. Two young saplings of *Quercus robur* have recently germinated in a spot where the ground cover of herbs, forbs, and low-growing *Salix glauca* was disturbed by reindeer trampling. The locality is a thermally favorable, south-facing slope, at the same altitude as the birch tree line, which has shifted 170 m upslope during the past century. Mount Predikstolen, 1055 m a.s.l. Photo: 19 August 2005.

FIGURE 2. A sapling of *Ulmus glabra* growing in treeless and closed meadow vegetation on a slope where the birch tree line has advanced 140 m over the past 100 years. Mount Laptentjakke, 990 m a.s.l. Photo: 16 June 2005.

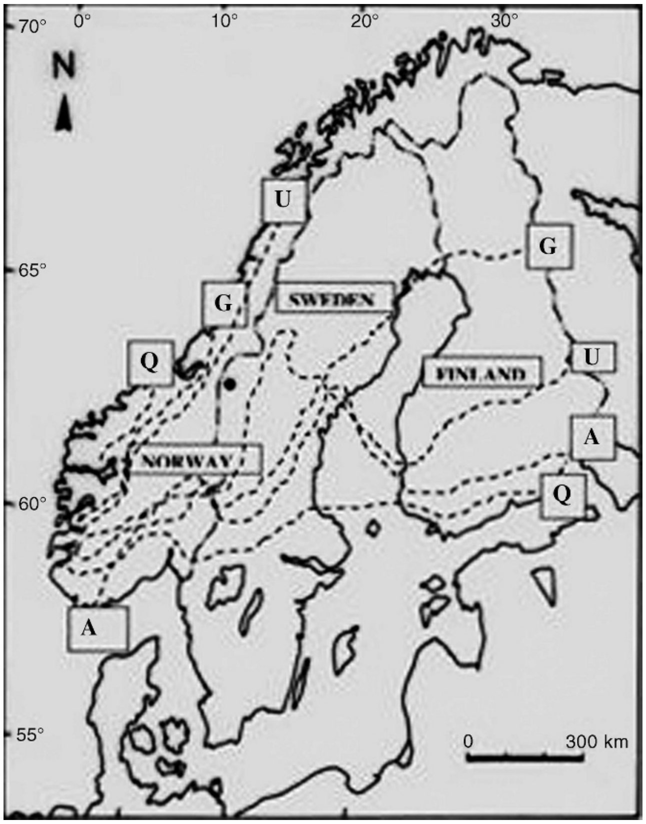

FIGURE 3. Map showing distribution limits for *Quercus robur* (Q), *Ulmus glabra* (U), *Alnus glutinosa* (G), and *Acer platanoides* (A). The study area is indicated by a black dot. Modified after Hultén (1971).

occasionally some specimens have attained a size of 5 m in nine growing seasons (Ove Johansson, personal communication), clearly attesting that the potential distribution limit is further north. Accordingly, the sapling limit has moved inland and northwards to reach at least 64°14′N, 12°22′E, 335 m a.s.l. during the past few years. Although less specifically studied, other thermophilic species are also currently naturalizing in the same geographical interval as *Quercus*, e.g. *Acer plantanoides*, *Corylus avellana*, and *Fraxinus excelsior*. Among these, *Acer platanoides* appears as the most expansive one, which relates to the fact that it is the most frequently planted ornamental tree in this group.

CLIMATE EVOLUTION

As indicated above, all saplings of thermophilic trees have germinated during the past 10–15 years, and none was recorded during earlier surveys of the transects; neither are they mentioned in the field-botanical literature from this region (e.g. Kilander, 1955). Thus, their current emergence is a recent phenomenon which should be evaluated in the context of the climate over the past 15 years, relative to some prior interval of equal or longer duration. Thus, relevant climatic parameters for the period 1991–2005 are compared with 1961–1990 (Table 2). All data refer to the official meteorological station Storlien/Visjövalen (see above), and are consistent with general trends for a much wider region of west-central Sweden (Alexandersson, 2006).

For all seasons, air temperature and precipitation have increased substantially, with a maximum for the winter and a minimum for the autumn. Precipitation has increased during all seasons, except for the autumn. A more detailed view on temperature evolution over the period 1991–2005 is provided in Figure 4 (A–D) for the different seasons separately. For spring (March–May), summer (June–August), and autumn (September–November) there is a tendency for rising temperatures, while the winter period (December–February) is more indifferent, although on a high level.

Between 1985 and 2005, the trends for root zone temperatures recorded at the tree line of *Pinus sylvestris* in the study area are +1.7 and +2.5 °C for the summer and winter, respectively (Kullman, 2007b).

Supporting proxy for exceptional climate warming during the past few decades is provided by anomalous local glacier recession (Kullman, 2004a, 2004b).

Discussion

It is clearly demonstrated that climate warming within the past few decades has been sufficient to evoke substantial range-limit extension (polewards and upwards) of broadleaved thermophilous tree species. The close causal association with rising temperatures is further supported by contemporary upshifts of

TABLE 2

Air temperature and precipitation changes during different seasons, expressed as means for the period 1991–2005 minus 1961–1990. Data provided by the Swedish Meteorological and Hydrological Institute (SMHI).

Season	Temperature change	Precipitation change
Spring (March–May)	+0.7 °C	+10%
Summer (June–August)	+0.7 °C	+20%
Autumn (September–November)	+0.4 °C	−10%
Winter (December–February)	+1.8 °C	+10%

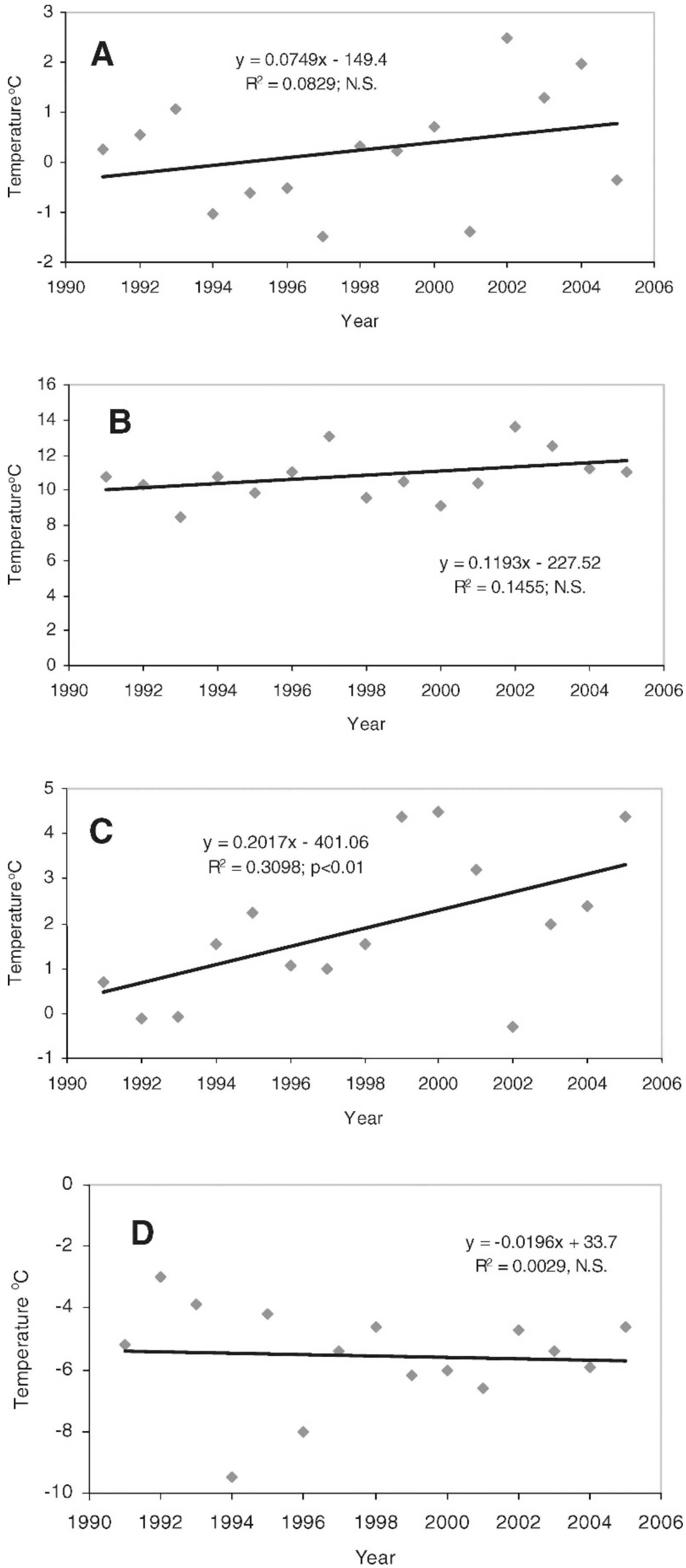

FIGURE 4. Seasonal mean air temperature evolution, 1991–2005, recorded at the Storlien/Visjövalen meteorological station. A = March–May, B = June–August, C = September–November, D = December–February.

most boreal tree species as well as subalpine and alpine plant species in the same area (Kullman, 2004a, 2007a).

The great extent and rate of both latitudinal and altitudinal migration seem virtually incomprehensible. However, casual observations, reported in the literature, can evidence that similar dispersal jumps of propagules actually take place. For example, fruits of *Acer pseudoplatanus* are reported from the surface of an alpine snow patch in the Norwegian mountains, more than 800 m higher than the nearest putative parent tree (Fremstad and Elven, 1996).

In different regions of Fennoscandia below the subalpine belt, expansion of thermophilic plant species were documented in concurrence with the distinct "warming pulse" in the 1930s–1940s (Blomqvist, 1933; Erkamo, 1956; Aas, 1970). These tendencies were halted or marginally reversed during several subsequent intervals when the warming trend ceased. This caused general stress to species growing close to their cold margins (Iversen, 1944; Kullman, 1997; Holtmeier, 2003).

Although repeatedly projected (see above), few studies have documented range expansion of plant thermophilies in Scandinavia in concert with the warming phase of the past few decades. However, Berger and Walther (2003) have evidenced northward expansion of *Ilex aquifolium* in southern Norway and Sweden, obviously related to warmer winters. Another example is *Crambe maritima*, which seems to expand northwards along the west coast of Norway in response to rising spring temperatures (Lundberg, 1996). In south and central Europe, advance of thermophilic trees and other plants northwards and towards higher elevations is ubiquitous (Walther, 2003; Penuelas and Boada, 2003).

The occurrence of thermophilic tree species in the zone at the present occupied by subalpine forest is certainly a novelty, although not entirely unique in a total Holocene perspective. In fact, firm megafossil evidence demonstrates that these and other warmth-demanding trees grew at corresponding high elevations during the temperature optimum of the early Holocene, about 9500–8000 years ago (Kullman, 1998, 2004c). Also, this first postglacial immigration happened surprisingly swiftly by long-distance dispersal and much faster than can be deduced from traditional pollen data studies (e.g. Huntley and Birks, 1983).

For the thermophilies concerned here, different life histories seem to be of minor importance with respect to dispersal ability (cf. Clark, 1998). For example, *Quercus* with relatively heavy fruits does not perform differently than wind-dispersed *Acer* and *Ulmus*.

The potential for rapid geographical displacements of plant species when climate ameliorates, as now evident from both paleobotanical and actual evidence, has to be taken into account in models of biogeographical evolution in a warmer future. These results stress that relevant modeling has to rely on empirical monitoring data, rather than static correlative approaches.

It needs to be stressed that the pioneering high-altitude thermophilies reported here are extremely few and of low frequency at the landscape level. Moreover, they are all tiny and still highly vulnerable to climatic and other disturbances. Thus, the warming trend needs to remain persistently on higher levels than today if these specimens should survive, attain tree size, and reproduce and if these species should become more conspicuous and permanent elements of mountain forests. Moreover, one cannot entirely exclude the possibility that saplings of the same group of species have occurred occasionally at these elevations during the past few millennia. Thus, the main importance of the current observations lies in the notion that migration delay does not necessarily hinder plant distributions to track climate change.

Acknowledgments

This study was defrayed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS). Comments by two anonymous referees are greatly appreciated.

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Ms accepted April 2007