Importance of mountain height and latitude for the altitudinal distribution limits of vascular plants in Scandinavia: are the mountains high enough?

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The main aim of the present paper was to study regional differences in the altitudinal distribution limits of vascular plants in relation to mountain height and latitudinal position. Altitudinal limits from previously studied areas were compared with the altitudinal distribution limits given by Lid and Lid (2005) as a reference. Based on these comparisons, different trend lines were used to evaluate the effects of mountain height and thereby estimate how high a mountain must be for vascular plants to reach their potential altitudinal limits. Study areas were Hardangervidda and Aurland in southern Norway, Jämtland in central Sweden, Lule Lappmark in northern Sweden, Troms in northern Norway and Graubünden in Switzerland. A regression analysis of the altitudinal limits for 177 vascular plants in Scandinavia compared with the same species in Switzerland gave a highly significant ($p < 0.001$) linear equation with a slope coefficient of 0.95 and a Y-intercept of 1057. Species limits in Hardangervidda, Aurland and Jämtland, however, showed non-linear altitudinal trends for the whole mountain ranges when they were compared with the highest recorded limits for the same species in Scandinavia. Differences between the recorded altitudinal limits from Scandinavia (mostly from the Jotunheimen mountains) and the same species from Switzerland were in average the same for lowland, boreal and high altitudinal species ($p > 0.422$). Comparisons within Scandinavia show that lowland/boreal and high altitudinal species showed different altitudinal distribution patterns. The position of the forest limit increased on average with 72.4 m per degree increase in latitude from Switzerland to northern Scandinavia. The altitudinal span of the alpine zone was approximately 1100 m in Switzerland and in Jotunheimen but considerably lower in the southern Scandinavian study areas. Studies of altitudinal distribution limits of vascular plants may give an indication of to what extent the height of a particular mountain influence plant distribution and thereby its vegetation zonation.

Keywords: Scandinavia, distribution limit, forest limit, mountain summits, climatic change

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Introduction

The altitudinal limit of a plant is often used as an indicator of its hardiness toward the extreme climatic conditions in high mountain areas, e.g. the Ellenberg temperature indicator value or the respiration value (Dahl 1998). If growth is not restricted by space, humidity or edaphic conditions, the altitudinal limits for vascular plants are in most cases constrained by too low summer temperatures. Both Arctic and alpine distribution limits are often found to be confined to areas where the mean temperature of the warmest month lies between 1.0 °C and 3.0 °C (Rannie 1986; Karlsen & Elvebakk 2003; Callaghan et al. 2004). For more than a century, altitudinal limits for vascular plants have

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been recorded in different parts of the world (e.g. Reisigl & Pitschmann 1958; Pauli et al. 1999). Not surprisingly, the highest limits have been recorded where the mountains are highest, and there the uppermost plants are often found several hundred metres below the summit (Grabherr et al. 1995; Körner 2003). In areas where the mountains are lower, several plants may be found on the mountain peak (e.g. Walther et al. 2005). On the highest mountains it is often reported that there is an exponential increase in species richness approximately 1000 m downwards from the uppermost occurrences of vascular plants (Grabherr et al. 1995; Nagy & Grabherr 2009).

Regional and world-wide comparisons of the altitudinal limit of forest trees have resulted in numerous scientific papers and text-books (e.g. Holtmeier 2003). In Scandinavia, forest limits reach their highest elevation in south central Norway (above 1200 m), but from there they decrease in all directions (e.g. Dahl 1998; Strand 1998). The decreasing trend from north to south does not follow the general trend of increasing summer temperatures (e.g. Aune 1993) as we should expect, but a significant decrease in maximum mountain height (e.g. Moen 1999) may possibly explain this deviation. Regional comparisons of maximum distribution limits of other vascular plant species have so far received little attention. Altitudinal limits for vascular plants can be given for any mountain, but their explanations are often difficult, as indicated by the extensive discussions on the causality of the altitudinal forest limits. Often it is of interest to know whether the actual species reach their maximum possible altitudinal limit within the actual geographic area.

Studies on summit floras and on plant altitudinal limits are becoming increasingly popular as a study approach, and one can mention at least three important reasons for this. Firstly, recorded altitudinal limits are frequently used as a basis for studies on altitudinal gradients in vascular plant species richness, where species richness is quantified as the number of species with altitudinal limits within 50 or 100 m elevation bands (e.g. Odland & Birks 1999; Grytnes & Vetaas 2002). The range of a species along an altitudinal gradient is geometrically constrained by the height of the mountain. This is an example of the so-called hard boundary (Colwell & Lees 2000), and the altitudinal variation in species richness is therefore highly influenced by the height of the actual mountain (Grytnes & Vetaas 2002). Secondly, previous studies on plant distribution limits are now being reanalyzed in order to find possible effects on climatic change (e.g. Klanderud & Birks 2003; Walther et al. 2005; Jurasinski & Kreyling 2007; Lenoir et al. 2008). Mountain height may in such studies influence the rate of potential invasion of new species. Thirdly, it is often assumed that high mountain areas may become refuges for many low competitive alpine plants with increasing global warming (e.g. Stanisci et al. 2005), and evaluations of floristic and ecological conditions in high mountain areas are therefore essential (Guisan & Theurillat 2000).

In general, there are three main factors that determine the altitudinal limits of vascular plants (Rahbek 1995; Dahl 1998; Körner 2000, 2003): (1) the height of the actual mountain determines the variation in climate and growing season length within the area; (2) the regional climate character is essential for plant distribution, and this is again generally a function of latitude and altitude, and; (3) the available mountain area and thereby also the variation in habitats are strongly related to mountain height.

In the Jotunheimen mountain range, the highest mountain is 2469 m, and here the highest recorded vascular plants limit is 2370 m (Lid & Lid 2005), which is approximately 1200 m above the forest limit. On the highest mountains we can expect to find a zone below the summit where no plants are growing, while on lower mountains (e.g. < 2000 m), several vascular plants may be found even on the summit. The height and total area of the alpine zone above the forest limit is considered to be of major importance for the vertical extent of the alpine zone and its species richness. Relationships between the altitudinal span of the alpine zone in relation to the mountain height are given for different European mountain areas by Ozenda (1988) and on a global scale by Körner (2003).

In a previous study (Odland 2009), the effect of mountain height on vascular plant species richness was investigated. In Aurland Western Norway, with a mountain height of 1764 m, it was shown that species richness within the 1500–1600 m elevation band was 41.0% lower, and the 1600–1700 m elevation band was 65.7% lower than within same altitudinal bands in Jotunheimen where the mountains are much higher. It was assumed that maximum mountain height and its effect on temperature conditions by the Massenerhebungeffekt could partly explain these differences in species richness. A strong effect of mountain height on species richness was also found by Stanisci et al. (2005) when they analyzed changes in species richness along the altitudinal gradient (2405 m versus 2730 m in the central Apennines, Italy). It was shown that 70% of the species did not reach the highest summit, and a drop in mean temperature was observed at soil level along the same gradient from 3.11 °C to 0.03 °C. The pattern of decreasing species richness along the altitudinal gradient in Aurland indicated that the effect of low mountain height was particularly strong at elevations less than approximately 400 m below the summit (Odland & Birks 1999; Odland 2009).

The effect of mountain massif height on plant life at high altitudes is also shown by the general altitudinal decrease in species diversity. In areas where the mountains are relatively low (< 2500 m), a linear decreasing trend in species richness has been found (Odland & Birks 1999; Odland 2009), while in areas where the mountains are much higher, exponential decreasing trends have been found (Grabherr et al. 1995; Körner 2003).

Åberg (1952) compared the altitudinal limits of species common to Lule Lappmark, northernmost Sweden, with Graübunden in Switzerland (data from Braun-Blanquet & Rübel 1932–1936), and the two series of extreme values were tested for their correlation. He found a strong correlation between the two series, a fact that was also taken as an estimate of the ecological significance of the species concept. The altitudinal limit of a certain species in Lule Lapmark was assumed to give an approximate measure of its hardiness also in Graübunden and vice versa. But he also emphasized that there may occur naturally exceptions caused by ecological differences and unequal distribution of alpine ecotypes. A species that in Lule Lappmark reached 1000 m a.s.l. should theoretically in Switzerland be found within an interval of 2497 ± 316 m a.s.l., while a species that in Switzerland reached 2500 should be found at 973 ± 235 m a.s.l. These differences were paralleled by the difference in the position of the forest limits. Åberg (1952) anticipated that the mountains in Lule Lappmark, reaching over 2000 m, were high enough allowing vascular plants to reach their climatic altitudinal limit. Dahl (1998) also compared altitudinal limits of plant species in Norway with their corresponding limits in the Alps, and on average the limits were situated approximately 1000 m higher in the Alps, a difference he also found to be paralleled by the altitudinal difference in the position of the climatic forest limit.

It is generally considered that effects of global warming will allow species to move upward and colonize new areas at higher altitudes, but high-mountain populations are expected to suffer from increased habitat fragmentation and increased competition with species from lower elevation areas (Walter et al. 2005). A 2–3 °C increase in temperatures may result in an advance upward by approximately 600 m (Grace et al. 2002). The rate to which such upward migration may happen depends, however, on available space and habitat surface (Guisan & Theurillat 2000; Theurillat & Guisan 2001). Sætersdal et al. (1998) state: "however, for some species, such as mountain plants, there may be nowhere for them to migrate because they are already at the top of the mountains." If the mountains are not high enough even boreal species may occupy the summits and creating a strong competition for available space, a competition that high altitudinal plants most likely will loose.

The main aims of this study are to compare the altitudinal distribution limits of vascular plants from different regions with the highest recorded values for Scandinavia as given by Lid and Lid (2005) as a reference. Two possible altitudinal trends will be tested: (1) if the limits of all included species show the same pattern in the study area as in the reference area, a linear altitudinal trend with a slope coefficient close to 1.0 should be found, and; (2) if we compare the differences in altitudinal limits for both lowland and for high altitudinal species between the two areas there should be no significant altitudinal trend, but for areas situated at different latitudes, the altitudinal limits should be displaced according to differences in temperature conditions. Both of these trends will be assumed to indicate that the actual mountain areas are high enough for all plants to reach their potential altitudinal limits within the actual study areas. Possible deviations from these null models will be discussed in relation to mountain height and the complex altitudinal environmental gradients.

Study areas, data, and methods

This study is based on previous floristic investigations from different mountain areas in Scandinavia (Fig. 1) where the altitudinal limits of vascular plants have been recorded. This is a comparative study, and the altitudinal limits for vascular plants within the different study areas are related to re-

Fig. 1. Geographic location of the study areas. Latitudinal position and other information from the study areas are given in Table 1. Graubünden Switzerland is not shown.

corded limits given by Lid and Lid (2005). Most species have their Scandinavian altitudinal limits within or in the vicinity of the Jotunheimen mountain massif, central Norway, but some have their limits in other mountain areas. A few limits were adjusted according to the highest records presented by Halvorsen and Salvesen (1983). Otherwise, the original records were retained even though some areas have re-sampled, and new limits have recently been found (Klanderud & Birks 2003; Kullman 2007; Moen & Lagerström 2008; Høitomt & Olsen 2010).

The following criteria have been used to select species to be used for the comparisons (see also Åberg 1952):

- the included species should be found from the forest limit ecotone and upward
- the species should be frequent, and have a relatively high ecological tolerance
- species taxonomy should be comparable; some taxa (subspecies and variants) are aggregated to reduce the risk of misidentification (cf. Åberg 1952; Moen & Lagerström 2008)
- introduced, anthropochorous species (cf. Dahl 1998) are omitted
- wetland species are omitted
- northern unisentric species in Scandinavia (cf. Dahl 1998) are omitted

In comparative studies between sites that are geographically widely separated, altitude per se is a poor environmental predictor. Therefore the altitudinal position of the forest limit is used as a "zero level" when regional altitudinal distribution patterns are compared (Körner & Paulsen 2004). The alpine zone is defined as the vertical zone between the forest limit and the mean altitudinal limit of the three vascular plants species with the highest record altitudes because some species may be found on extreme heights in microclimatic favourable sites.

Species recorded within the study areas in Scandinavia are separated into three groups according to their maximum altitudinal limits: (1) lowland species not recorded above the forest limit, (2) boreal forest species with a max limit approximately 500 m above the forest limit, and (3) high altitudinal species reaching the highest summits (more than 500 m above the forest limit).

The data from Hardangervidda represent several years of floristic inventories published by Lid (1959). The study area cover most parts of the Hardangervidda mountain plateau with mountains up to 1719 m high. The climatic forest limit varies from approximately 1000 m in the west to 1100 m in the south-eastern part. Some new limits published by Halvorsen and Salvesen (1983) have been included. The data from Aurland (Odland 1991, 2009; Odland & Birks 1999) represents floristic inventories during two summers supplied with earlier published records. The floristic data from Jämtland covers extensive studies on several mountain tops in the south-western part of central Sweden, on the border with Norway (Kilander 1955). Some of the mountains here have been resampled (Kullman 2007; Moen & Lagerström 2008). Kullman (2007) showed that the forest limit had increased and that the flora had changed on the summits. 17 species were lost and 57 had established on at least one mountain since the 1950s. A majority of the species had changed their altitudinal distribution within the range of ± 50 m, but some even more. The changes were assumed to be results of climatic change, reindeer grazing and hikers. Åberg (1952) compiled lists of altitudinal limits from Lule Lappmark, northernmost Sweden from different sources. This is a mountainous area with 7 peaks higher than 2000 m. He maintained that these were sufficiently high to permit even the most high-altitudinal species to reach their climatic limit. Engelskjøn and Skifte (1995) measured altitudinal limits of vascular plants in the district of Troms in northern Norway. The study summarizes data from the whole county, sampled during a long period of time. Several mountains on the northern border between Sweden and Norway reach 1700 m. Åberg (1952) gave distribution limits also for the same species from Graubünden Switzerland based on previous published floristic data. Based on these data, Åberg (1952) compared the distribution limits of species between north Scandinavia and the Alps. In the two northernmost areas, only few lowland species have been included.

Regression analyses and lowess trends (degree of smoothing = 0.5, number of steps = 2) were performed by the MINITAB program.

Results

Some general data and results from the study areas are presented in Table 1. Differences in mountain height, species limit, alpine zone limit and position of the forest limit along the latitudinal gradient from 46 °N to 69 °N are shown in Fig. 2. The south-north trend lines showing the general decrease in forest limit (1) and alpine zone limit (2) are drawn on the basis of data from Graubünden and Jotunheimen as given in Table 1. In total, the altitudinal difference in the position of the forest limit between the study areas is 1600 m. The climatic forest limit in Switzerland lies 1130 m higher than the highest forest limit in Scandinavia, and in Troms in north Norway the forest limit lies 470 m below this limit. In Hardangervidda, Aurland and Jämtland the limits are lower than the general trend suggests, and in these areas the summits are relatively low (Fig. 2). The altitudinal difference between the summit and the uppermost occurrences of vascular plants in the Alps is obviously much greater than in Scandinavia. This indicates that in case of climatic changes, there is limited space available for plant uplift. The altitudinal difference between

Table 1. General data and results from the study areas. Switz = Graubünden Switzerland, Scand = Scandinavia (Jo = Jotunheimen mountain massif where most species reach their max limits), H = Hardangervidda, A = Aurland, Jä = Jämtland, LL = Lule Lappmark, T = Troms. (2) = Total number of species recorded from the study area used in the comparisons. (6) = Highest mountain in the study area. (7) = Altitudinal position of the climatic forest limit. (8) = Difference between the highest forest limit in Scandinavia (Jotunheimen) and the other study areas. (9) = Altitudinal difference between mountain summit and position of the forest limit. (10) = Maximum altitudinal recorded vascular plant limit. (11) = Altitudinal limit for the alpine zone, as defined by the mean distribution limit for the three species with the highest altitudinal limits ± SD (Standard Deviation). (12) = Number of plants found at the highest mountain (summit). (13) = Altitudinal difference between summit and uppermost plant limit (6–10). (14) = Vertical range of the alpine zone (11–7).

	Switz.	Scand.	H	A	Jä	LL	T
(1) Latitude °N	46.5	61.5	60.2	60.8	63.0	67.0	68.6
(2) No vascular plants studied	177		350	189	252	176	292
(3) No lowland plants	50		35	15	0	0	0
(4) No boreal plants	74		173	80	72	20	41
(5) No high altitudinal plants	53		142	94	180	156	251
(6) Max mountain height (m)	4057	2469	1710	1764	1796	2001	1717
(7) Max forest limit altitude	2350	1220	1100	1150	880	800	750
(8) Diff. forest limit	+1130		–120	–70	–340	–420	–470
(9) Diff. summit-forest limit altitude (6–7)	1893	1249	610	614	916	1201	967
(10) Max limit vascular plants	3560	2370	1690	1764	1782	1900	1700
(11) Mean max 3 vasculars ± SD (Alpine zone limit)	3443 ± 132	2357 ± 12	1694 ± 5	1764 ± 0	1778 ± 17	1800 ± 95	1700 ± 0
(12) No vasculars at the summit	0	0	8	10	1	1	3
(13) Diff. summit-max limit vascular plants (6–10)	497	99	20	0	14	101	17
(14) Alpine zone range (11–7)	1093	1137	594	614	898	1000	950

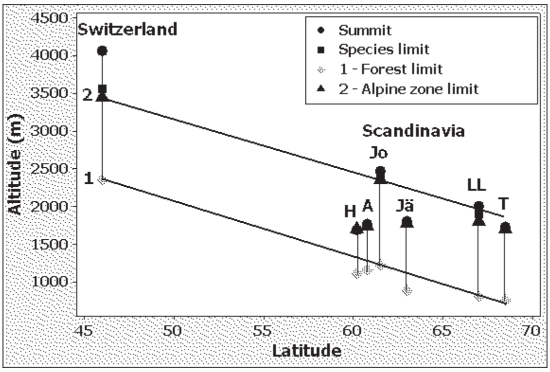


Fig. 2. Relationships between some altitudinal limits measured within the study areas and their position along the latitudinal gradient (legends as in Table 1). General trend lines are drawn from Graubünden Switzerland to Jotunheimen southern Norway and extended northwards to Troms northern Norway. Line (2) shows the decrease in the altitudinal limit of the alpine zone, and line (1) shows the altitudinal position of the forest limit.

the forest limit and the mean limit for the three highest-growing vascular plants in the Alps may also give an indication of the vertical range that could be available for plant growth if all vascular plants should reach their climatic distribution limit. In the Alps this range is close to 1100 m (Table 1, no 14), and also nearly the same in Jotunheimen where most plants have their highest limit in Scandinavia. In terms of temperature, this vertical range represents a range of approximately 6 °C calculated on the basis of a lapse rate of 0.6 °C per 100 m increase in altitude. In Lule Lappmark and Troms the altitudinal spans reach almost the same values, while in Hardangervidda, Aurland and Jämtland the spans are much smaller.

Comparisons of altitudinal distribution limits

Altitudinal limits for species recorded in Switzerland are in Fig. 3A plotted against their maximum limits in Scandinavia. The figure shows that most plants included respond in the same way, i.e. that both lowland and high altitudinal species show the same altitudinal trends, but that the general trend line is displaced in altitude due to differences in latitude (and climate). The linear altitudinal trend has a slope coefficient 0.95 (Table 2) which indicates a high parallelism between the distribution limits for all plants between these areas. The y-intercept is –1057 m which close to the difference in forest limit (1130 m) (Table 1). In Hardangervidda and Aurland, the scatter-plots indicate not-linear altitudinal trends as shown by lowess lines (Fig. 3B, 3C). The altitudinal limits for the high altitudinal plants are here obviously constrained by the mountain height which in these areas are lower than 1800 m (Table 1). The boreal species lie here in general 100–150 m lower than in the reference data (Table 2). Up to an altitude of approximately 1600 m, however, the comparative altitude records follow linear trends with slope coefficients close to 1.0 (Table 2). The altitudinal pattern is quite similar in Jämtland (Fig. 3D) and here the boreal species follow a linear trend with a slope coefficient of 0.86. The altitudinal limits in the northernmost areas, Lule Lappmark (Fig. 3E) and Troms (Fig. 3F), follow linear functions with a regression slope coefficients close to 0.8 for all species (Table 2.)

Differences in altitudinal limits between the studied areas

Differences between altitudinal limits given in Lid and Lid (2005) and for the same species in the ac-

Table 2. Results of linear regression analyses where the maximum limits of vascular plants in the different study areas (y) is given as a linear function of the max limit in Scandinavia (x). Ranges of max limits of the included species within the different areas in Scandinavia are given. N = Number of species used. * = Regression based on lowland and boreal species only.

Area	Equation	R2	P	N	Max limit var.
Switzerland	Y = 0.95 * x + 1057	88.3	< 0.0001	177	925 – 2370
Hardangervidda	Y = 1.00 * x – 116	72.2	< 0.0001	208	900 – 1590*
Aurland	Y = 1.00 * x – 156	76.6	< 0.0001	93	850 – 1620*
Jämtland	Y = 0.86 * x – 59	72.2	< 0.0001	183	940 – 1780*
Lappmark	Y = 0.76 * x – 142	73.3	< 0.0001	176	925 – 2370
Troms	Y = 0.85 * x – 365	78.8	< 0.0001	292	900 – 2370

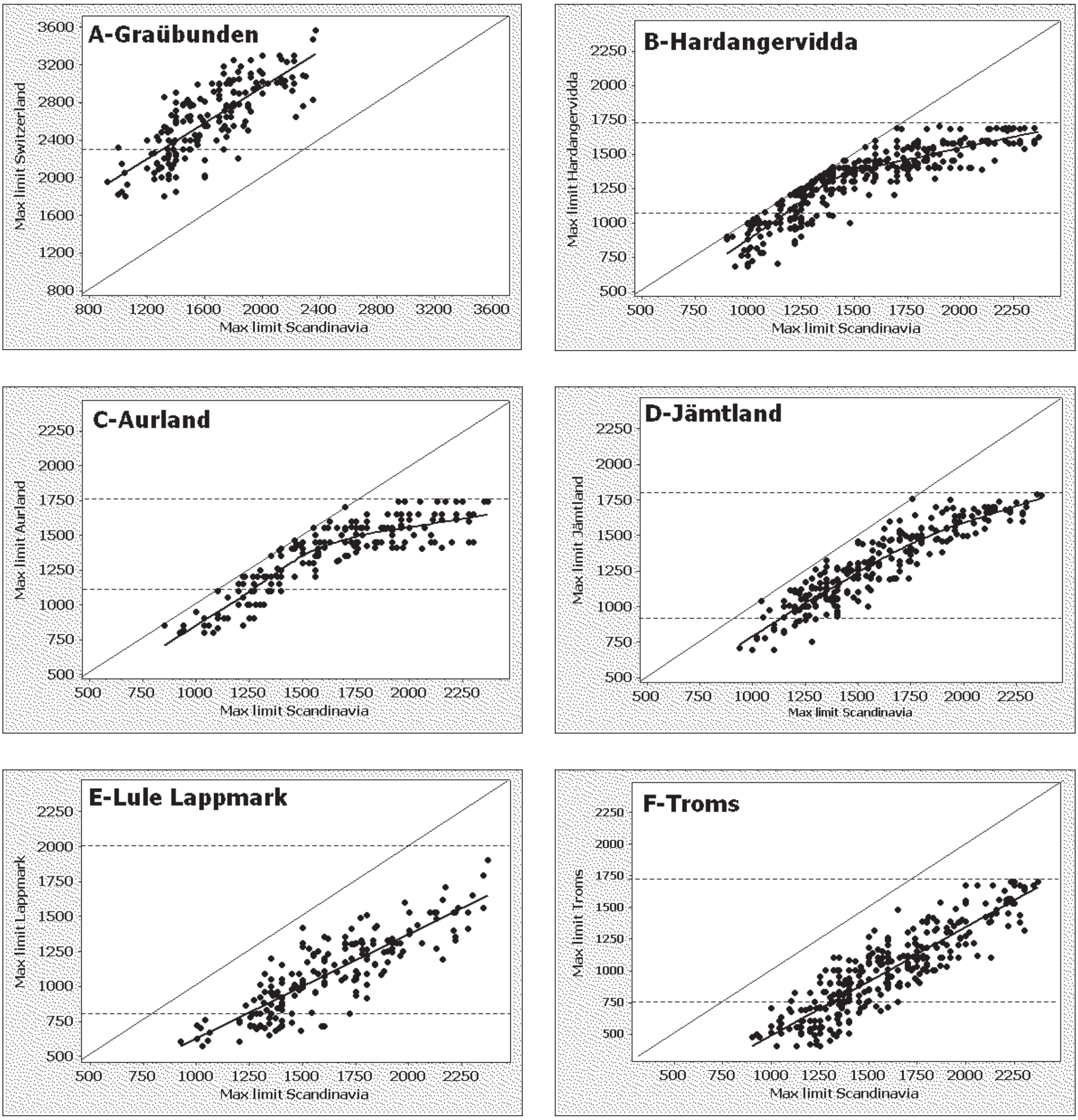
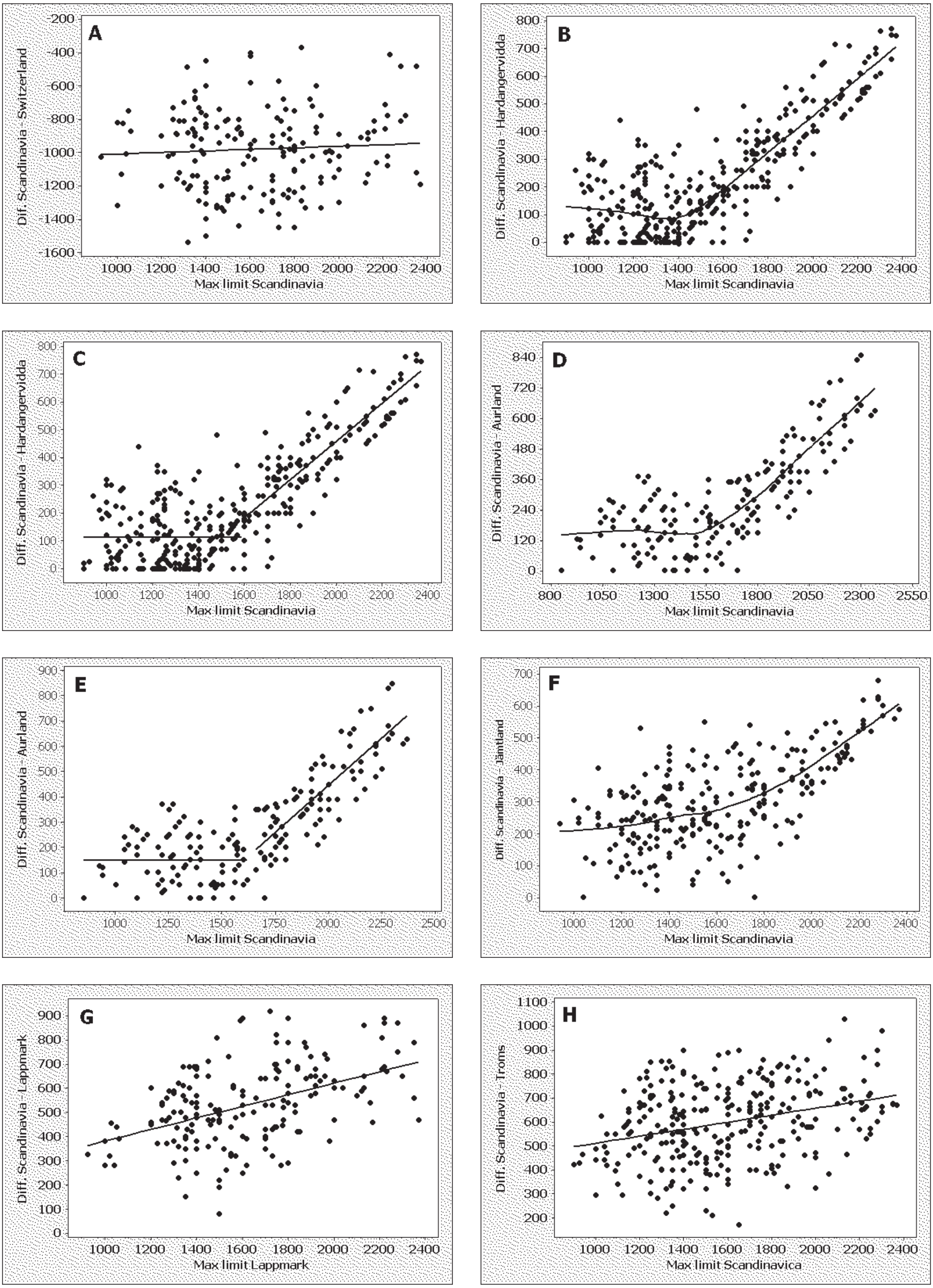


Fig. 3. Max limits for vascular plants in Scandinavia as given by Lid and Lid (2005) compared with the max recorded limits for the same species from the actual study areas. Dotted lines show maximum mountain altitude (not shown for Graübunden) and maximum forest limit altitude. Some comparisons show significant linear trends, while others show deviations from a linear trend, especially for high-altitudinal species. A null-model suggests that the trend line should follow a straight line with a slope coefficient close to 1.0, but with a displacement according to differences in latitude (regional climate). Fig. 3A. Switzerland; the linear regression line is drawn, and the equation is given in Table 2. Fig. 3B. Hardangervidda; the actual altitudinal trend is shown by a lowess line. Lowland and boreal species follow a linear trend with a slope coefficient close to 1.0 (Table 2). Fig. 3C. Aurland; the actual altitudinal trend is shown by the lowess line. Lowland and boreal species follow a linear trend with a slope coefficient close to 1.0 (Table 2). Fig. 3D. Jämtland; the actual altitudinal trend is shown by the lowess line. Lowland and boreal species follow a linear trend with a slope coefficient of 0.86 (Table 2). Fig. 3E. Lule Lappmark; the altitudinal trend for all species is shown by a linear regression line with a slope coefficient of 0.76 (Table 2). Fig. 3F. Troms; the altitudinal trend for all species is shown by a linear regression line with a slope coefficient of 0.85 (Table 2).


A
Diff. Scandinavia - Switzerland
-200
-400
-600
-800
-1000
-1200
-1400
-1600
1000 1200 1400 1600 1800 2000 2200 2400
Max limit Scandinavia
B
Diff. Scandinavia - Hardangervidda
800
700
600
500
400
300
200
100
0
1000 1200 1400 1600 1800 2000 2200 2400
Max limit Scandinavia
C
Diff. Scandinavia - Hardangervidda
800
700
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100
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1000 1200 1400 1600 1800 2000 2200 2400
Max limit Scandinavia
D
Diff. Scandinavia - Aurland
840
720
600
480
360
240
120
0
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Max limit Scandinavia
E
Diff. Scandinavia - Aurland
900
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Max limit Scandinavica

Table 3. Results of linear regression analyses of the altitudinal difference between plant limit in the reference area (Max Scandinavia) in relation to the max limit in the study area. N = Number of species used. Regression analyses of species within Hardangervidda, Aurland, and Jämtland were performed on two data sets: (1) = lowland and boreal species only, and (2) = high altitude species only. Variations in the max limits in Scandinavia are given for the species included in the regression analyses.

Area	Equation	R^2	P	N	Max limit var.
Switzerland	$Y = 0.047 * x - 1057$	0.40	0.422	177	925 – 2370
Hardangervidda (1)	$Y = -0.003 * x + 116$	0.00	0.942	208	900 – 1590
Aurland (1)	$Y = -0.005 * x + 156$	0.00	0.936	93	850 – 1620
Jämtland (1)	$Y = -0.002 * x + 221$	0.00	0.900	72	940 – 1370
Hardangervidda (2)	$Y = 0.69 * x - 918$	74.5	< 0.0001	142	1600 – 2370
Aurland (2)	$Y = 0.75 * x - 1048$	68.4	< 0.0001	94	1650 – 2370
Jämtland (2)	$Y = 0.32 * x - 218$	37.9	< 0.0001	180	1380 – 2370
Lappmark	$Y = 0.24 * x + 142$	21.4	< 0.0001	176	925 – 2370
Troms	$Y = 0.15 * x + 365$	9.8	< 0.0001	292	900 – 2370

tual study areas are shown in Fig. 4. Fig. 4A shows that there is no significant altitudinal trend if we compare limit differences for the same species recorded in Switzerland and in Scandinavia. There may be major differences in altitudinal limits for some species, but these differences show no overall significant trend. This indicates that the lowland, the boreal, and high altitudinal species show the same altitudinal trend. In average, the vascular plants have their altitudinal limits 1057 m higher in Switzerland, and this difference equals the forest limit differences between these areas (Table 1).

The study areas in Scandinavia show deviating patterns. The altitudinal trends in Hardangervidda (Fig. 4B), Aurland (Fig. 4D) and Jämtland (Fig. 4F) are shown by lowess lines. Boreal species are mostly found less than 400 m below their maximum limits in Scandinavia while high-altitudinal species are found 700–900 m lower than their altitudinal limits in Scandinavia.

By splitting the Hardangervidda distribution data into two floristic groups; 208 lowland and boreal species and 142 high altitudinal species, different trends appear (Fig. 4C). Lowland and boreal species are here in average found 116 m below their altitudinal limit in Scandinavia, and these show no altitudinal trend. The difference between the forest limits shows almost the same value (Table 1). For the 142 high altitudinal species, there is a strong linear altitudinal trend ($R^2 = 74.5$) which shows that the difference between their limits in Hardangervidda and Scandinavia increase strongly with their ability to grow at very high altitudes. Similar trends are also found for species in Aurland (Fig. 4E) and Jämtland areas (Table 3).

Fig. 4. Plots showing the difference between the max altitudinal limit of a plant in the actual study area compared with the max altitudinal limit in Scandinavia as given by Lid and Lid (2005). A null-model suggests that if there is no effect of too low mountain height, a scatter-plot should follow a horizontal line (no altitudinal trend) with a y-intercept altitudinally displaced according to the difference in the general climatic condition between the areas. In Switzerland (Fig. 4A), there is no significant altitudinal trend ($p = 0.422$). The maximum limits lie in general 1057 m higher in Switzerland than in Scandinavia, and the difference is on average the same for species with different altitudinal limits. In Hardangervidda (Fig. 4B), Aurland (Fig. 4D), and Jämtland (Fig. 4F) the differences follow non-linear altitudinal trend as shown by the lowess lines. High altitudinal species are within the study areas found 700–900 m lower than the max limits given in Lid and Lid (2005), while the differences are much smaller for lowland and boreal species. By splitting the species into two groups, two patterns emerge: lowland and boreal species show no altitudinal trend, while the high-altitudinal species show strong linear altitudinal trends ($p < 0.0001$) as shown by the data from Hardangervidda (Fig. 4C) and Aurland (Fig. 4E). Equations are given in Table 3. Within Lappmark (Fig. 4G) and Troms (Fig. 4H) the altitudinal differences increase for all species with increasing max altitudinal limits (Table 3).

In the two northernmost areas (Lule Lappmark and Troms), all species show significant altitudinal trends (Fig. 4G, 4H). High altitudinal species are mostly found 800–900 m lower in these areas compared with their max limits in Scandinavia, while lowland and boreal species are mostly found approximately 400 m lower than their max limits in Scandinavia. The significant linear altitudinal trends show a decreasing slope coefficient from south to north, which may indicate a decreasing effect of too low mountain height northwards (Table 3).

Discussion

When we compare altitudinal limits for plants from different areas we should expect to find major variations both on a local scale (neighbouring mountains) and on a broad geographic scale (different region or country). The most obvious reasons for such variations are related to differences in climate, mountain height, total area, and edaphic factors (bedrock, substrate and habitat variation) (e.g. Moser et al. 2005). There may, however, also be effects related to different opinions about species taxonomy and possible ecotypes within a taxon. Some species are also naturally rare, and the chance of finding such species at their uppermost occurrences is low (Åberg 1952). Differences in sampling effort can also be important, and one can not assume that time spent within each area is equal (Åberg 1952; Engelskjøn 1994; Moen & Lagerström 2008). Time lag between sampling year and possible environmental changes during this period may also represent a source of error (e.g. Grabherr et al. 1995; Walther et al. 2005). Despite these possible sources of error it is assumed that the general trends found in this study gives important information about ecological effects of mountain height and latitude between the investigated mountain areas.

Scattered outposts of vascular plants are reported from very high altitudes (6400 m in the central Himalayas), often in microhabitats whose thermal regime is similar to the more common situation far below. Körner (2003) therefore maintains that altitude per se becomes a doubtful criterion for estimating conditions for life in high mountains. Below the uppermost outposts of higher plants, species richness increases with decreasing altitude. In both tropical and temperate mountain areas, the altitudinal interval between the uppermost occurrences and the uppermost closed vegetation may approach 1000 m. From this elevation, there may be an additional 1000 m down to the forest limit (Grabherr et al. 1995). To reduce the effect of extreme outposts, the mean value for the three highest records of vascular plants has been used here (Table 1).

Effects of mountain height and space

For both species richness and species distribution limits along altitudinal gradients, it has been maintained that there is a strong species-area relationship (e.g. Rahbek 1995). This is because area and habitat diversity are closely linked, and therefore number of species increases generally with area. In the Alps, areas above 4000 m include less than 0.03% of the area at 2000 m. Unfavourable climate combined with a strong reduction in available land area will therefore constrain plant growth and species richness on the highest mountain peaks (Körner 2000). The height of the mountain may therefore be used as a proxy for available area variation in habitats and total variation in climate (cf. the Massenerhebung effect, Holtmeier 2003; Odland 2009). Differences between mountain height and distribution limits of vascular plants are shown in Fig. 2. The values vary from close to zero in some of the studied areas to 497 m in Graubünden, Switzerland. Grabherr et al. (1995) present the similar values for some high mountain areas in the world: Kilimanjaro (5896 – 5760 = 136 m), Himalaya (8848 – 6400 = 2448 m), Andes (7084 – 5800 = 1284 m) and the Alps (4807 – 4450 = 357 m). In Scandinavia this interval lies between 0 and 101 m (Table 1 no 13). This shows that the areas which today lie above the upper limit for vascular plants is very small in Scandinavia, and consequently the available space for plant growth in case of future temperature increase is very limited.

Relationships between mountain height, latitude, forest limit and species limits

Due to the general patterns of decreasing temperatures from south to north, most organisms show decreasing altitudinal limits along the same geographic gradient, and this includes also the forest limits. It is assumed that both the polar and alpine forest limit have a bioclimatic characterisation (Jobaggy & Jackson 2000; Holtmeier 2003; Körner & Paulsen 2003; Nagy 2006). The climatic forest limit in an area may therefore be used as a reference to which other distribution limits can be compared, but the height of the mountains should always be considered.

According to Körner (2003), the distance between the forest limit and snowline varies mostly between 800 m and 1600 m, with a mean of about 1100 m, and this range roughly corresponds to the altitudinal range of the alpine zone. In Jotunheimen, the snowline lies at approximately 2200 m, i.e. 1000 m above the forest limit. In the other areas it has been difficult to estimate the position of the snowline because of the low mountain heights (Åberg 1952).

The altitudinal span of the alpine zone is 1093 m in Graubünden (Table 1 no 14). If we use the position of the climatic forest limit as a bioclimatic indicator, this indicates that the upper limit of the alpine zone lies in Switzerland at an altitude where the mean July temperature is approximately 6 °C lower that at the forest limit. If we assume that the species limit and forest limit both in Graubünden Switzerland and Jotunheimen represents climatic limits, the lines (1) and (2) in Fig. 2 indicate that the position of the forest limit in Hardangervidda, Aurland and Jämtland lie much lower than the general latitudinal trend suggests. Dahl (1998) emphasized the importance of the mountain height for the altitudinal distribution limits for plants, and he maintained that no climatic timber-line could be recognized unless there were, in the neighbourhood, mountains that exceed the climatic timber-line by at least 200 m. This study indicates, however, that the mountain height has to be much higher than this if the forest should reach its potential altitudinal limit. In Lule Lappmark and Troms, however, the forest limit position seems to reach its potential altitude, but not all the high altitudinal species. The forest limit in Troms lies 1600 m lower than in Graubünden (Table 1), and this gradient represents a geographical span of 22 °N latitude. The general trend is then a 72.4 m decrease in altitude of the climatic forest limit for each degree increase in latitude. Similar latitudinal trends have been reported after forest limit studies elsewhere. In the northern Appalachian, the alpine tree line decreases from 1480 m at 44 °N to 550 m at 55 °N which corresponds to an 83 m increase for every 1° increase in latitude (Cogbill & White 1991). Malyshev (1993) measured decreases between 70 m and 90 m per degrees for various transects in northern Asia, and Körner (1998) found by a linear regression of the tree line altitude/latitude relationship between 70 °N and 45 °N a general decrease of 75 m per degree increase of latitude. Fairly similar results have also been found in different parts of the world (e.g. Crawford 1989; Gorchakovsky 1989; Sveinbjörnsen 2000). Schickhoff (2005) studied the relationship between latitudinal and altitudinal position of forest limits on the Himalayan south slopes, and he found a general decrease of 68 m for each degree increase in latitude, but the variation was considerable, probably due to both variable mountain heights and variation in humidity.

General latitudinal trends of decreasing forest limits and the vertical extension of the alpine zone have been shown both for Europe (Nagy 2006; Nagy & Grabherr 2009) and globally (Körner 2003). According to Nagy and Grabherr (2009), there appears to be a general linear decrease in the forest limit altitude from the Alps (c. 2600 m at 41 °N) to the Scandes (c. 600 m at 69 °N). They consider the upper limit of the tree line ecotone to lie at about 1300 m in southern and at 600 m in northern Scandinavia.

The altitudinal span between the forest limit and the upper limit of the alpine zone as defined here is shown in Table 1 (no 14) and Fig. 1. This indicates that the mountains in Hardangervidda, Aurland, and Jämtland are far too low to give the high altitudinal plants possibilities to reach their potential altitudinal limits. Also the mountains in Lule Lappmark and Troms appear to be too low. It is therefore possible that the forest limit isohypses in parts of Scandinavia as shown in Dahl (1998), Moen (1999) and Heikkinen (2005) are strongly modified by mountain heights, and that they regionally could be situated at higher elevations if the mountains were higher.

Variations in the distribution limits of vascular plants

Differences between altitudinal limits for plants between the study areas and the reference records also show different altitudinal trends. When the limits from Switzerland and Scandinavia are compared, a highly significant linear trend with a slope coefficient close to 1.0 was found. This shows that, despite major variations, species with limits at different altitudes show the same altitudinal trend, and from this we may infer that both lowland and high altitudinal plants, in general, reach their potential limit in both these areas. The nonlinear altitudinal trends in Hardangervidda, Aurland and Jämtland may be interpreted as a result of the low mountain height. Lowland and boreal species follow, however, closely a linear regression lines with a slope coefficient close to 1.0, indicating that the low mountain height does not influence their altitudinal distribution limit.

Comparisons of differences in species limits between the study areas have revealed three different patterns: (1) no trend for the whole altitudinal range (Scandinavia and Switzerland); (2) no altitudinal trend for lowland and boreal species, but an increasing trend for the high-altitudinal species (Hardangervidda, Aurland and Jämtland), and; (3) increasing trend with increasing altitudes along the whole gradient (Lappmark and Troms). This indicates that species with different distribution limits have similar trends along the whole gradient when comparing Switzerland and Scandinavia. In Aurland, Hardangervidda and Jämtland, however, high altitudinal species do not reach their potential altitudinal limits. Lowland and boreal species do not appear to be influenced by the low mountain height. In Lappmark and Troms no such pattern was found because few (less than 8) lowland and boreal species were included in the study. Table 3 shows that the linear regression slope coefficient and the R^2-values decrease strongly from south to north in Scandinavia which may indicate that the general effect of too low mountain height decreases northwards. The relatively low slope coefficients in Lule Lappmark and Troms as shown in Table 2 and Fig. 3E and 3F indicate also that the mountains there are too low for all vascular plants to reach their potential altitudinal limits.

Implication for species distribution in a warmer world

Predictions of effects of climatic warming assume an upward migration of plants resulting in a change of their altitudinal distribution limits. We may therefore expect a strong competition for the limited space one the mountain tops in the future (Guisan & Theurillat 2000; Walther et al. 2005; Parolo & Rossi 2008). As an example, Sanz-Elorza et al. (2003) found that high mountain grasslands were replaced by shrubs from lower altitudes in the central Iberia Peninsula. It may be tempting to apply the general relationship between temperature and altitude to claim that a 3 °C increase in temperature will result in an altitudinal advance of approximately 500 m, both for the forest limit and for other vascular plants. There are, however, numerous reasons why we can not use this general relationship for a particular area, and the main constraint will often be lack of available space (see review by Theurillat & Guisan 2001). Theurillat and Guisan (2001) calculated that an increase of 3.3 K in mean air temperature, corresponding to an altitudinal shift of 600 m in the European Alps, would on average reduce the area of alpine vegetation by 63% and the nival zone would by 81%. For Scandinavia we should expect even higher reductions of these zones due to the low mountain height. It can, however, not be assumed that species and plant communities may find equivalent surface areas with similar physiographic conditions when shifting upwards in elevation. Theurillat and Guisan (2001) assume therefore that an increase of 1–2 K in mean temperature may not shift the present forest limit upwards by more than 100–200 m. The study of Moen and Lagerström (2008) indicates, however, that major changes in the summit flora can result from impacts other than climate change. Grazing of semi-domestic reindeer, sheep and tourist hiking may locally change the natural vegetation composition. Therefore, generalizations on possible future changes on the summit flora based on climatic change are difficult. Each species and each mountain area should be evaluated individualistically.

Conclusions

This study presents a method whereby the effect of mountain height on the altitudinal distribution limits of vascular plants and also on the position of the forest limit can be evaluated. The method requires records of vascular plants distribution limits in the actual mountain area and similar data from a reference regional area where plants are assumed to reach their max potential distribution limits. Comparisons between distribution limits from Switzerland and Scandinavia indicate that even the highest mountain massif in Scandinavia, (Jotunheimen, central south Norway) is just sufficiently high to allow all plants to reach their present potential maximum limits, while the Lule Lappmark mountains (northern Sweden) are close to being high enough. In the other studied areas, the mountains are estimated to be 200 to 600 m too low for the high altitudinal species to reach their potential limits. Effect of low mountain height in parts of Scandinavia will be increasingly important in the future due to climate change and thereby a stronger competition for space on the summits.

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