

Rapid spread of a fleshy-fruited species in abandoned subalpine meadows - formation of an unusual forest belt in the eastern Carpathians

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In recent decades, most subalpine hay meadows and pastures have been abandoned, and trees have been recolonizing these sites where forest existed before agricultural activity. This study examined how woody vegetation, dominated by the deciduous fleshy-fruited tree *Sorbus aucuparia* (rowan), expanded on subalpine meadows in the Western Bieszczady Mountains (eastern Carpathians, Poland) after the cessation of agricultural use. The aims were to determine the abundance of rowan in the woody vegetation, to estimate the rate of rowan expansion in the studied area, and to characterize the variability of rowan stands and growth forms. Rowan dominated the current plant community of abandoned subalpine meadows, though this species is not considered a rapid colonizer of open areas and was not frequent in the uppermost forest belt before the colonization. The whole area was encroached by rowans in a very short period of time 60-70 years ago. Rowan tree density was similar throughout the elevational gradient but the growth form changed, becoming more shrub-like with increasing elevation. Rowan stands will likely be the main element of the subalpine belt in this region in the upcoming decades. At present, no tree species can be considered a rapid successor to rowan in the area.

Keywords: Abandoned Subalpine Meadows, Forest Recolonization, Land Use Change, Subalpine Forest, Succession of Woody Vegetation

Introduction

Recent studies on vegetation of European mountains reported the re-establishment of the forest in subalpine meadows where the upper forest limit was formerly shifted downward by human activity (Kozak 2003, Bolli et al. 2007, Holtmeier & Broll 2007, Gehrig-Fasel et al. 2007, Tasser et al. 2007, Bryn 2008, Albert et al. 2008, Sitko & Troll 2008, Chauchard et al. 2010, Weisberg et al. 2013). It is thought that forest expansion in the subalpine belt is primarily due to land use changes in the last century, mainly the abandonment of hay meadows and pastures. However, the effect of climate change can not be excluded, since favorable climatic conditions may facilitate fo-

rest encroachment into subalpine scrubland and grassland (Gehrig-Fasel et al. 2007, Weisberg et al. 2013).

Carpathians subalpine forests cover an elevation range from about 1200-1500 to 1250-1650 m a.s.l. (Zarzycki 1963, Sitko & Troll 2008), and are mostly formed of *Picea abies* (L.) H. Karst., accompanied in some areas by other coniferous species: *Larix decidua* Mill., *Pinus cembra* L. and *Pinus sylvestris* L. The uppermost forest belt may also include deciduous tree species, mostly beech (*Fagus sylvatica* L.) and less frequently sycamore (*Acer pseudoplatanus* L.), birches (*Betula pendula* Roth and *B. pubescens* Ehrh.), or rowan (*Sorbus aucuparia* L.). During the expansion of subalpine fo-

rest, the most dynamic changes usually occur along the timberlines composed of conifers such as *P. abies* (Sitko & Troll 2008), *Pinus uncinata* Ram. (Camarero & Gutiérrez 2004) or *L. decidua* (Didier 2001) which are anemochorous species. Over the entire Carpathian range, *F. sylvatica* forest is less responsive to favorable climatic changes and agriculture cessation than coniferous forests, resulting in a relatively stable timberline (Kucharzyk 2004, Weisberg et al. 2013).

Generally, tree species colonizing subalpine non-forest areas are those belonging to the uppermost forest belt (Albert et al. 2008, Holtmeier 2009, Chauchard et al. 2010), with several exceptions. Sitko & Troll (2008) found abandoned meadows above the anthropogenic beech timberline in the Ukrainian Carpathians commonly colonized by wind-dispersed spruce. An unusual situation occurs also in the Western Bieszczady Mountains (eastern Carpathians, Poland), where the cessation of agriculture also led to the recolonization of abandoned meadows by the forest, though its species composition is different as compared with those prevailing in the uppermost forest belt. Indeed, the anthropogenic upper forest limit was previously formed by beech forests with small admixtures of *A. pseudoplatanus* and *S. aucuparia*. Such meadows were first colonized by *Alnus viridis* (Chaix) DC. in LAM. & DC.

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(Schramm 1958, Zarzycki 1963). Surprisingly, after about 70 years of secondary succession, rowan was the woody species that expanded most abundantly in the subalpine belt of the Western Bieszczady Mountains (Durak et al. 2013, 2015). In particular, rowan is currently the dominant species in some areas of this region, resulting in the formation of a new forest belt above the former upper limit of beech forests (Fig. 1).

In this study, we examined two aspects of rowan stand formation after colonization of abandoned subalpine meadows in the Western Bieszczady Mountains, namely: (i) how quickly rowan has spread over meadow areas; and (ii) what was the structure of stand after approximately 70 years of recolonization. The specific aims of this study were to: (1) determine the abundance of rowan in the woody vegetation that developed in abandoned subalpine meadows; (2) estimate the rate of rowan expansion; and (3) examine the variability of rowan stand and growth form characteristics in relation to habitat conditions.

Methods

Study site

The study was conducted in the subalpine area of the Western Bieszczady Mountains (eastern Carpathians, southern Poland), where the original vegetation was likely made by scattered clumps of *S. aucuparia* and *A. viridis* stretching from the natural upper timberline (1150-1260 m a.s.l. – Zarzycki 1963) to the mountain top (up to 1350 m a.s.l.). Starting since 15th century, pastures and hay meadows have been created by clearcut, determining a shift downward of the natural timberline. Such deforestation activity ended in the middle of the 19th

century: in the 1940s the agricultural use of subalpine meadows in the Western Bieszczady Mountains was completely abandoned, and woody vegetation began to encroach (Kucharzyk & Augustyn 2012). In 1973, the whole area was included into the Bieszczady National Park and became part of the Eastern Carpathian International Biosphere Reserve in 1998.

The study area comprised the subalpine belt of the Bukowe Berdo ridge (49° 6' 0" N, 22° 43' 50" E, 1238 m a.s.l.). According to archival cadastral maps, this area was used as pasture for cattle in 1852 and in later decades. Agriculture in this area was moderately intensive, and further decreased after World War I. Indeed, some scrublands are reported on the Bukowe Berdo ridge on the 1937 map, suggesting that the abandonment of subalpine meadows in this area started earlier than in other parts of the region (Kubijowicz 1926, Kucharzyk & Augustyn 2008, 2012).

The study site encompassed approximately a 22-hectare area of a former subalpine meadow, now largely colonized by rowan stands, just above the beech timberline that represented the upper forest limit before the abandonment. The site stretched over the NE and SW slopes of the massif (mean slope: 18.5°; range: 5-35°), from the sheltered vicinity of the beech forest limit to the most elevated places of the mountain ridge (range 1111-1214 m a.s.l.). Soil type varied across the study site, with dystric cambisols at lower elevations and lithosols, regosols, rankers and umbric rankers at higher elevations closer to the ridge (Skiba et al. 1998). Only the area where rowan saplings were present was considered in this study.

Study species

S. aucuparia (Rosaceae, Maloideae) is a deciduous monoecious fleshy-fruited tree living up to 100-150 years and reaching 15-20 meters in height (Kullman 1986, Hofgaard 1993). Seeds are dispersed by animals, mainly birds (Raspé et al. 2000). In central European highlands, rowan occurs from foothills up to subalpine scrubland at 2000 m a.s.l., in various forest types and different climatic and edaphic zones (Schaminée et al. 1992, Raspé et al. 2000). Rowan is usually a minor component of the plant communities, reaching fairly higher frequencies in species-poor coniferous forests or disturbed stands (Hofgaard 1993, Holeksa & Zywiec 2005), where it may colonize newly-formed gaps (Zerbe 2001, Jonášová & Prach 2004). This process largely relies on the recruitment from seedling and sapling banks established before gap formation (Zywiec & Ledwon 2008, Zywiec & Holeksa 2012).

Data collection

A regular grid (100 × 100 m) of 23 circular plots (0.01 ha) was established in the study site in 2012 (Fig. 2). Plots were positioned with GPS (accuracy 2-3 m) and characterized in terms of several topographic and habitat parameters. Plot aspect and slope were measured in the field using a compass and a clinometer. Elevation was derived from a digital elevation model (GRID with cell size 5 m). The soil type was determined on the basis of a soil map (Skiba et al. 1998). The distance between each plot and the upper limit of the beech forest was measured using an aerial photo.

Within each plot, individuals of all woody species were counted and characterized by their height, the number of shoots (longer than 5 cm) per individual, and the diameter of each stem at breast height (dbh). Youngest seedlings (height <5 cm) were not included in view of their high mortality and problems with their detection (due to low stature). Tree species nomenclature followed Mirek et al. (2002).

For each plot, the age of the five thickest rowans was measured, under the assumption that the thickest ones were the oldest. Trees were cored with an increment borer (diam. 5 mm) at ca. 30 cm above the ground. The cores were mounted on wood slats, dried and progressively polished with a belt sander (up to grid 600) to make the tree ring sequences clearly visible. The samples were scanned at a resolution of 2400 dpi and annual rings were counted using the WinDendro[®] software (Regent Instruments 2012).

Data handling and analysis

Prior to statistical analysis, the plot aspect was converted from the azimuth values (decimal degrees) into values ranging from -1 to 1 using the formula $\sin(\alpha - \pi/2)$, where α represents the azimuth value given in radians. This transformation produced a continuous variable, whose maximal



Fig. 1 - Vegetation belt dominated by rowan tree stand on the Bukowe Berdo ridge (eastern Carpathians, southern Poland).

and minimal values corresponded to opposite facing slopes: N (-1) and S (1). This variable was assumed to represent the gradient of microclimatic conditions in the sampling area. A categorical variable was used for soil type, with value "0" for initial soils such as lithosols, regosols, rankers and umbric rankers, or "1" for more developed soils, i.e., dystric cambisols.

For each plot, tree density and total basal area (per hectare) were calculated for each woody species. For rowan, the density of all shoots (per hectare) was also determined. The relative number of individuals and relative basal area of each woody species in each plot (100 m²) were also calculated. Basal area was calculated using the dbh of all stems taller than 1.3 m. The age of the oldest rowan tree sampled at a given plot was taken as the approximate time of tree establishment. We recorded the maximum height, mean stem diameter, mean number of stems per individual (at ground level) and mean number of twigs per stem (at breast height) of live rowans in each plot.

Non-normally distributed data (continuous variables) were transformed using logarithmic or exponential functions, according to Okland et al. (2001). To explain the variability of rowan tree stand and growth form characteristics, multiple regressions were performed using the following predictors: aspect, elevation, slope and soil type. Significant predictors were identified using a forward stepwise selection procedure.

Results

Tree stand characteristics

The studied stand was mainly formed by rowan, which averaged 81.7% (range: 36.4-100%) of all tree individuals per plot. Other tree species were *A. pseudoplatanus* (10.4%), *F. sylvatica* (3.5%), *A. viridis* (3.4%), *Abies alba* Mill. (0.6%), *P. abies* (0.2%) and *Salix silesiaca* Willd. (0.2%). Rowan basal area averaged 18.4 m² ha⁻¹ (range: 3.6-34.3 m² ha⁻¹), accounting for 90.3% (range: 28.1-100%) of the total stand basal area. The density of rowan trees ranged from 300 to

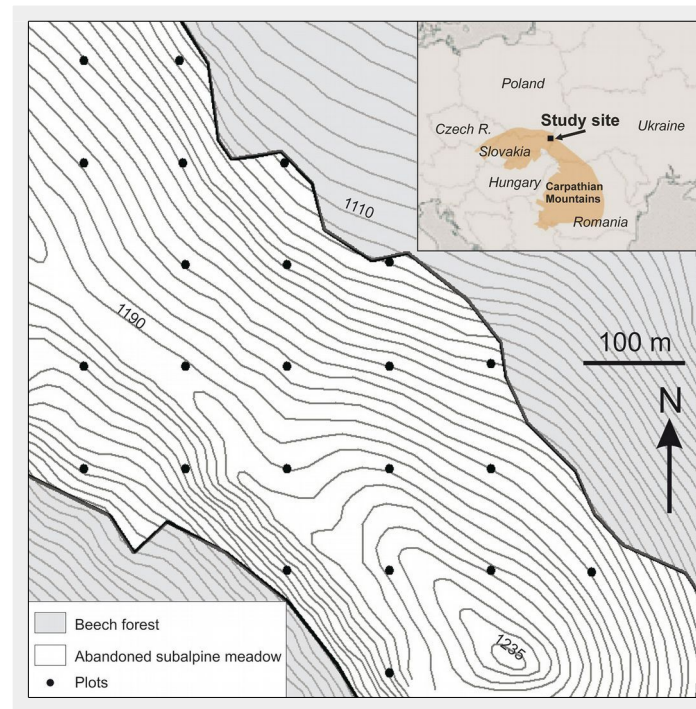


Fig. 2 - The regular grid of plots established in the studied area.

2700 individuals ha⁻¹ (mean: 1330 ind. ha⁻¹), and the density of rowan shoots ranged from 500 to 27 100 ha⁻¹ (mean: 6990 ha⁻¹). Stand age, as indicated by the age of the oldest rowan tree, ranged from 57 to 75 years (mean: 65 years). Some of the tree stand characteristics were highly correlated (Appendix 1).

In a preliminary analysis, Pearson's correlation tests were used to explore the strength of associations between variables within the explanatory data set (environmental variables) and response data set (rowan variables - Appendix 1). This analysis showed that plot elevation was strongly correlated with the distance between plots and the edge of the beech forest ($r=0.62$; $p<0.002$). The nature of the relationship between these parameters and rowan variables suggested that plot elevation is a causative variable. Therefore, the distance to the edge of the beech forest was selected and excluded from further analysis to reduce multicollinearity in the envi-

ronmental data.

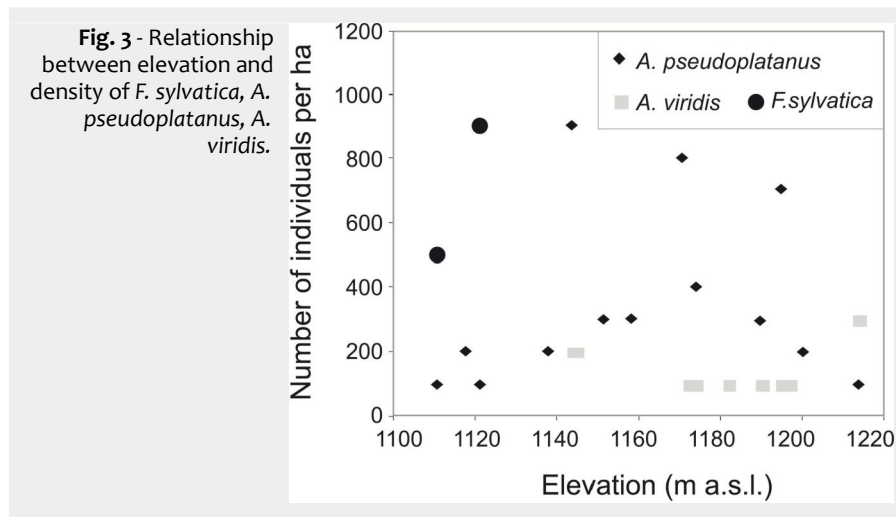
Multiple regressions showed that almost all stand characteristics were independent of the environmental variables (Tab. 1). Only the density of rowan shoots was significantly associated to a topographic gradient, increasing with elevation. Elevation also seemed to affect the distribution of some other species. For example, *F. sylvatica* was present only at lower elevations close to the upper limit of the beech forest, whereas *A. viridis* was absent from the lowest plots (Fig. 3). However, the total share of non-rowan species in the total number of tree individuals and the total stand basal area was the same regardless of elevation.

Rowan growth form

The diameter of rowan individuals averaged 7.4 (range: 1.3-16.5 cm) and the maximum height of individuals averaged 9.7 (range: 4.5-17.5 m). The mean basal area of rowan ranged from 36.1 to 422.9 cm² ha⁻¹ (mean: 171.4 cm² ha⁻¹). The mean number of

Tab. 1 - Effects of plot parameters on the characteristics of rowan tree stand and growth form illustrated by standardized (Beta) coefficients of multiple regression. (R^2_{adj}): adjusted R^2 ; (F): the F ratio; (p): significance level; (-): variable was not included in the model; (*): $p < 0.05$; (**): $p < 0.01$; (***) : $p < 0.001$.

Group	Dependent variable	Regression summary			Beta coefficients			
		R^2_{adj}	F	p	Aspect	Elevation	Slope	Soil
Tree stand	Age of oldest rowan	2.7	1.3	0.294	-	-	0.271	0.228
	SD of age of oldest rowans	4.0	1.5	0.255	-	0.213	-0.252	-
	Density of live rowans (ind. per ha)	10.2	3.5	0.075	-	-	-0.378	-
	Density of rowan shoots (per ha)	33.9	4.8	0.012	-	0.731**	-0.254	0.435
	Percentage of species other than rowan	7.6	1.9	0.176	-	-0.552	-	-0.338
	Percentage of species other than rowan in total basal area	14.7	2.9	0.078	-0.316	-0.344	-	-
Growth form	Total basal area of rowans (m ² ha ⁻¹)	3.0	1.7	0.208	-	-	0.273	-
	Mean basal area of individuals	28.9	9.9	0.005	-	-	0.567**	-
	Maximum height of individuals (m)	57.1	10.8	<0.001	-	-0.790**	0.307	-0.205
	Mean dbh of individuals (cm)	53.2	9.4	<0.001	-	-0.850***	0.172	-0.222
	Mean number shoots per individual	17.7	3.4	0.055	-0.276	0.428*	-	-
	Mean number of twigs per stem	34.4	12.5	0.002	-	0.611**	-	-



shoots per individual averaged 5.5 (range: 1-13.5) and the mean number of twigs per stem averaged 78.8 (range: 4-399). Some of the rowan growth form characteristics were highly correlated (Appendix 1).

In contrast to tree stand characteristics, rowan growth form clearly varied along environmental gradients. In multiple regression analysis, environmental variables accounted for 17.7 to 57.1% of the variation

in growth form characteristics of rowan. Elevation was the most influential factor, that negatively affected mean shoot diameter and the associated maximum height, and positively affected the mean number of twigs per shoot at breast height and mean number of shoots per individual (Tab. 1, Fig. 4). As regards other explanatory variables, slope had a positive effect on mean total basal area, while the effect of aspect and soil type was not significant.

Discussion

Rowan was the main woody species encroaching on the studied meadows along the whole elevational gradient. Moreover, rowan dominated on both the NE and SW slopes of the massif, from the beech forest limit to the mountain ridge. Similar situations have been reported in other abandoned subalpine meadows on Western Bieszczady Mountains (Winnicki 1999, Durak & Zywiec 2013, Durak et al. 2015). This kind of forest community is quite uncommon in the scientific literature. In the subalpine zone of the Massif Central in France, Schaminée et al. (1992) described scrub communities dominated by *Sorbus* species on abandoned pastures, with *S. aucuparia* being the most common species. Borysiak (1985) found both shrublands and woodlands formed by rowans at the natural upper forest limit on the Babia Góra Massif (western Carpathians, Poland). Kullman (1986) reported a high frequency of rowan trees in the subalpine zone of the Scandes in Sweden. Subalpine communities with only a small admixture of rowan in the woody species composition were reported more frequently (Motta 2003, Šibík et al. 2005, Zywiec et al. 2013).

Before their abandonment, subalpine meadows in the study area bordered the forest dominated by *F. sylvatica*, with small admixtures of *A. pseudoplatanus*, *P. abies*, *A. alba* and *S. aucuparia* (Schramm 1958, Zarzycki 1963). Soon after abandonment, scrubland dominated by *A. viridis* grew above the forest limit, with *S. aucuparia*, *A. pseudoplatanus*, *S. silesiaca* and *Rosa pendulina* being less frequent (Schramm 1958, Zarzycki 1963). All these species still occur in the vegetation on the abandoned meadows, though rowan became dominant since 1990 (Winnicki 1999) and now is largely the most abundant species, in particular in terms of basal area. The role of rowan in the stand increased significantly with elevation, which suggests that this species is more able to colonize subalpine meadows than any other woody species present in the area. This is surprising because rowan was rare in the studied meadows in the 1950s and 1960s, and because its mode of dispersal by animals (mainly birds) does not facilitate the fast colonization of large open areas. Hill et al. (1992) showed rowan invading abandoned hill pastures at sites located in the close vicinity of bird perches. However, it is possible that birds were not the main seed dispersers in the studied

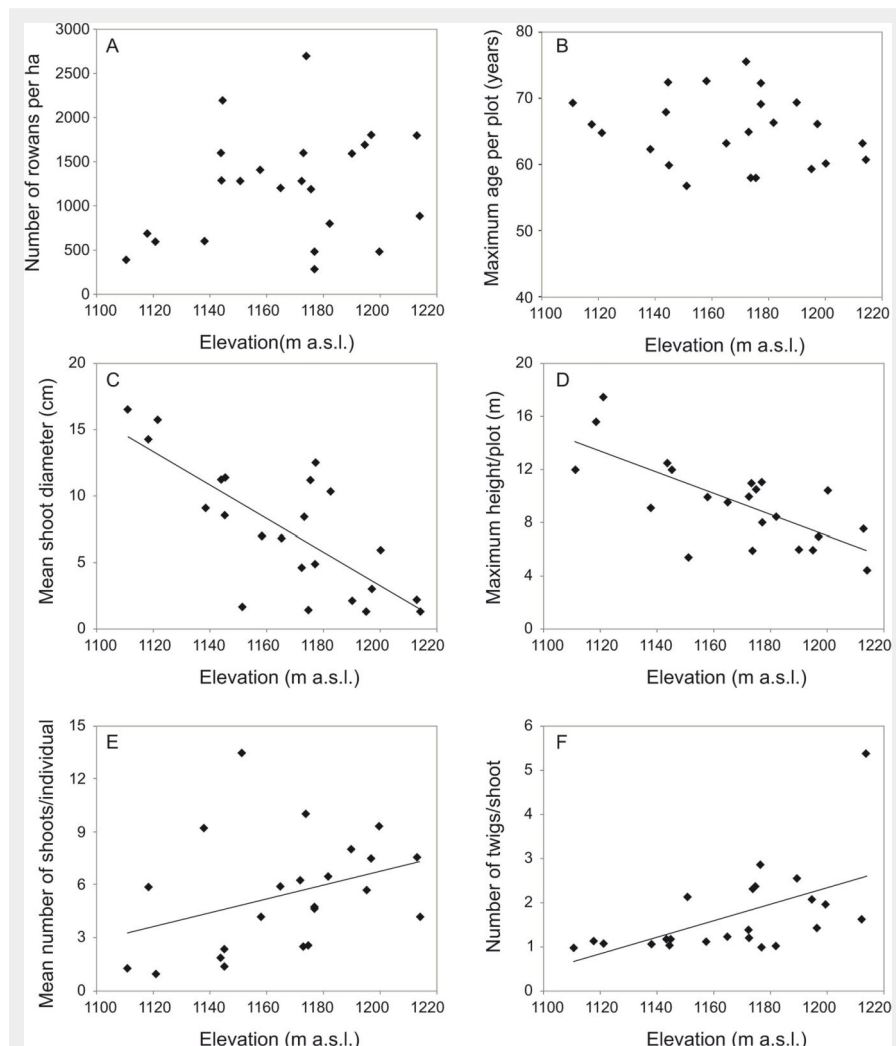


Fig. 4 - Relationship between elevation and: (A) rowan tree density; (B) age of oldest rowans in the plot; (C) mean shoot diameter; (D) maximum height of rowan trees; (E) mean number of stems per rowan tree; and (F) mean number of twigs per stem at breast height.

area. Rowan seeds could have been supplied as a result of past pasture management practices and the former presence of livestock. In this case, rowan regeneration may have started in the meadow area long before its abandonment. Ungulates can be effective seed dispersers (Jaroszewicz 2013), facilitating seedling emergence by trampling and exposing the bare soil, by reducing competition with grasses, and by promoting upslope migration as seed dispersers. Unlike mowing, grazing may facilitate seedling establishment in grassland (Cairns & Moen 2004, Julien et al. 2006). In an experimental study it was found that intense grazing by sheep increased rowan seedling recruitment (Hester et al. 1996). Rowan can survive for decades under suppression and grazing pressure, due to its ability to replace dead stems with new ones (Zywiec & Holeksa 2012). This ability gives it an advantage over the other woody species in the area, and could have supported the presence of a rowan population in subalpine meadows before abandonment.

In the studied subalpine meadow, rowan expanded at approximately the same time along the entire elevational range, covering areas from the sheltered vicinity of the beech forest limit to exposed fragments on the mountain ridge. The recorded age of the oldest rowans differed only slightly between plots, and their mean age matched the time since the abandonment of meadows. These findings might be explained in two ways. The first hypothesis is that the seeds were dispersed and seedlings were established throughout the whole area at the same time. This assumes that the probability of seed supply and seedling establishment was high and equal throughout the whole area. This seems unlikely, as rowan is considered a slow colonizer of open areas (Zywiec & Ledwon 2008). Moreover, the dispersal by animals usually results in a very uneven distribution of seeds and seedlings (Schupp 1993, Clark et al. 1998). The second explanation is that seedling development in the meadow vegetation was inhibited by adverse biotic or abiotic conditions. Most likely the inhibiting factor was pastoralism. Rowan seedlings lasted under grazing pressure in pasture vegetation for a long period of time, and their vertical growth accelerated when such pressure ceased. Under this second scenario the age of individuals should differ, but this difference could not be detected in this study as we took core samples at 30 cm above the ground, i.e., a height threshold not reached by woody plants growing in pastures. In the case of long-term persistence under grazing pressure, the growth increments at ground level would hardly ever show the real age of individuals. As rowan could survive under grazing pressure, it was likely that suppressed individuals accumulated over time (Zywiec & Holeksa 2012). Previous works have shown that young rowans can

markedly increase their growth rate after suppression ceases (Hester et al. 1996, Zywiec 2008). All these features of the regeneration strategy of rowan make the second explanation much more probable. Whatever the case of seedling establishment, rowan tree stands expanded in the studied area almost simultaneously, as evidenced by the narrow range of ages of the measured trees.

In this study, density of rowan trees did not decrease with increasing elevation and distance to the forest limit and decreasing distance to the mountain ridge. This result suggests that environmental conditions are suitable for regeneration and growth along the whole elevational gradient, confirming the broad edaphic and climatic amplitude of rowan. This species is adapted to a short growing season in that it stops shoot growth early, allowing buds to harden before freezing (Barclay & Crawford 1982, Raspé et al. 2000) and tolerates an extremely low stem water potential corresponding to the minimum values in sclerophyllous plants (Vogt & Lösch 1999). Furthermore, rowan bears mechanical damage very well, forming the wound periderm rapidly (Woodward & Pocock 1996), and it has a high vegetative regeneration capacity (Kullman 1986). Indeed, plants are often multi-stemmed and the sprouting mechanism can very effectively extend their lifespan (Zywiec & Holeksa 2012). All these features facilitated rowan survival in the harsh conditions of the mountain ridge.

The rowans' growth form changed along with elevation. At higher elevations rowans were shorter, their stems were thinner, and they had more shoots per plant than at lower elevations; in other words, they were more compact and more shrub-like. This trend is well known in mountain woody species (Bolli et al. 2007, Holtmeier 2009). Short-stature plants are less affected by temperature and snow cover better protects low-growing plants from freezing (Holtmeier 2009). A multi-stemmed form and the ability to sprout are important features enabling the rowan to survive the harsh mountain conditions, especially close to ridges. Vegetative reproduction by stump sprouts gives an advantage under stem breakage by wind, avalanches or heavy snow loads (Bellingham & Sparrow 2000, Holtmeier 2009). Rowan shows high sprouting ability (Kullman 1986, Zywiec & Holeksa 2012), and multi-stemmed individuals can survive for decades or longer through shoot turnover.

An interesting question is whether the rowan tree stands will be a long-lasting forest formation in this area, or rowan is rather only a pioneer species which will be displaced by other woody species in the long run. In other Carpathian ranges, rowan trees are usually overtopped and replaced by spruce, and it is reported that young spruces take advantage of improved soil conditions resulting from deposition of rowan litter (Emmer et al. 1998). At pre-

sent, no tree species can be considered a quick successor of rowan in the subalpine area of the Bieszczady mountains. It is most probable that beech stands will expand and replace rowans, though this will take a very long time due to constraints on dispersal of beech nuts. In fact, we recorded this species only in the lowermost plots. However, beech forest is thought to have covered the mountain ridges up to 1250 m a.s.l. until the 15th century (Kubijowicz 1926, Palczynski 1962). Another candidate for replacing rowan is sycamore, which was recorded on every second plot with similar frequency along the whole elevational gradient but with much lower abundance. Its seeds are dispersed by wind and can easily reach anywhere in subalpine areas. However, *A. pseudoplatanus* is less shade tolerant than *F. sylvatica* (Niinemets & Valladares 2006). It has been found that more shade tolerant species can maintain foliage in deeper shade, support larger leaf area indexes and harvest more light (Niinemets 2010). It might be hypothesized that coexistence would be more probable if light demanding rowan grows together with moderate shade tolerant sycamore than with very shade tolerant beech. Such mixed rowan-sycamore stands are well known in the Polish Carpathians (Michalik & Szary 1997, Matuszkiewicz 2001). Therefore, we hypothesize that rowan or mixed rowan-sycamore stands will be most likely the main element of the subalpine belt in this region in the upcoming decades.

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Supplementary Material

Appendix 1 - Pearson's correlation coefficients for tree stand and rowan growth form data.

Link: Durak_1470@supplo01.pdf