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Continuously missing outer rings in woody plants at their distributional margins

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ABSTRACT

Woody plants growing in seasonal climates normally form one growth ring each year. However, under severe stress conditions they may not complete annual wood production all the way down to the root collar resulting in continuously missing outer rings at lower stem sections (CMORs). Here we test whether CMORs occur at different distributional margins of woody plant species, where stress levels are expected to be high. We tested 13 species (202 individuals) of trees and shrubs growing at elevational and latitudinal shrub- and tree-lines, under conditions that are normally associated with a reduction of radial growth such as drought, cold or nutrient deficiency. Samples were collected from Alaska, north western Russia, Central Europe, Scandinavia and south eastern Spain. Annual radial growth was measured along several disks or cores of each individual applying the serial sectioning technique. Individuals of nine species showed CMORs. The proportion of individuals with CMORs within a sampled species and site ranged from 0% to 80%. The number of CMORs within an individual increased with decreasing sampling height on the stem. Significant correlations existed between the amount of CMORs and (i) cambial age, (ii) stem length, (iii) stem proportion/length below peat surface, and (iv) herbivore-caused defoliation intensity depending on the species and sampling location. Our results suggest that CMORs can be associated with a cambium that may be inactive, yet functional, for up to 18 years. We conclude that CMORs can occur in a wide variety of species, growth forms and biomes, suggesting a general strategy of woody plant growth. To avoid miss-dating in dendrochronological studies, we further recommend the use of the serial sectioning technique for woody plants growing in unfavorable environments, above all, when sample size is limited and when no established chronology for cross-dating is available.

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Introduction

Sampling of woody material for age determination or other dendrochronological analyses is usually performed at a certain stem height. This sampling height can vary from breast height (1.3–1.4 m), traditionally applied in forestry and dendrochronology, to ground surface in the case of smaller individuals, or even be at the root collar if exact age determination is aimed for. The underlying assumption is that a woody plant growing in a seasonal climate will form one growth ring per year from the tip of

the branches to the root collar. This implies that in a living individual, the outermost ring is the growth ring formed in the year of sampling or in the year before sampling if the new growing season has not yet started.

However, there are three types of deviation from this rule: (1) locally missing rings (LMR), where one or more growth rings are missing in some part(s) of the plant; (2) totally missing rings (TMR), where a plant does not produce wood anywhere in a specific year, and (3) continuously missing outer rings at the stem base (CMORs). This means that the last several growth rings of an individual are missing at the stem base or lower portion of the stem, but that they can be present higher up the stem.

LMRs have been frequently reported, generally resulting from drought stress in woody plants (Stokes and Smiley, 1968; Schweingruber, 1996). TMRs have not been reported widely (but see Novak et al., 2011) because it is necessary to analyze several

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Table 1
Tree and shrub species from different extreme environments and their position within the landscape analysed for this study.

Site characteristic	Species	Lat/Long	Elevation (m asl)	Aspect, slope
Elevational shrubline	<i>A. crispa</i> , Alaska	N 63°24', E 148°51'	963	185°, 5°
	<i>B. nana</i> , Alaska	N 63°45', W 148°51'	1200	225°, 20°
	<i>B. nana</i> , N-Sweden	N 68°21', E 18°41'	700–1100	170–185°, 5–25°
	<i>J. nana</i> , Alaska	N 63°44', W 148°51'	1010	160°, 25°
	<i>J. nana</i> , N-Sweden	N 68°21', E 18°41'	700–1100	170–185°, 5–25°
	<i>P. mugo</i> , Czech Republic	N 50°45', E 15°40'	1330–1470	45°/135°/225°, 5–45°
	<i>S. alaxensis</i> , Alaska	N 63°32', W 150°05'	1150	135°, 17°
	<i>S. glauca</i> , N-Sweden	N 68°21', E 18°41'	700–1100	170–185°, 5–25°
Elevational treeline	<i>B. pubescens</i> Ehrh. ssp. <i>czerepanovii</i> , N-Sweden	N 68°21', E 18°41'; N 68°29', E 18°44'	700	90°/180°, 5–15°
	<i>B. pubescens</i> Ehrh. ssp. <i>czerepanovii</i> , N-Sweden	N 68°27', E 18°54'	630	225°, 10–25°
	<i>B. pubescens</i> , NW Russia	N 67°22', E 62°11'	80	0°, 0°
Latitudinal treeline	<i>P. glauca</i> , Alaska	N 67°57', W 161°40'	166	180°, 5°
	<i>P. obovata</i> , NW Russia	N 67°22', E 62°11'	78	0°, 0°
Wet hydrological limit	<i>B. pubescens</i> , N-Sweden, mire	N 68°20', E 18°50'	520	0°, 0°
	<i>P. sylvestris</i> , Finland	N 62°32', E 30°29'	148	0°, 0°
Dry hydrological limit	<i>P. pinea</i> , SE Spain	N 38° 6', W 0°40'	5	0°, 0°
	<i>P. halepensis</i> , SE Spain	N 38° 6', W 0°40'	5	0°, 0°
Permafrost influences soils	<i>P. glauca</i>	N 65°52', W 149°25'	95	0–5°
	<i>P. mariana</i> , Alaska	N 66°15', W 147°47'	101	0°
		N 65°52', W 149°25'	95	0°

stem and branch disks of a particular woody plant to discover TMRs.

CMORs, on the other hand, have been reported notably from trees growing in suppressed conditions under a closed forest canopy (Niklasson, 2002), from trees with soil accumulation around the lower stem (Peters et al., 2002), which often form adventitious roots (DesRochers and Gagnon, 1997; Parent and Morin, 2002), from (prostrate) shrubs (Kolishchuk, 1990; Hallinger et al., 2010; Hallinger and Wilmking, 2011) or from woody plants affected by combinations of some of these factors (Parent and Morin, 2002). In these cases, simple ring count at stem base or the apparent root collar often did not reveal the true age of an individual (Kneeshaw and Claveau, 2001; Parent and Morin, 2002; Peters et al., 2002; Loeffers and Stadt, 2003; Hallinger et al., 2010). True age could only be determined by additional analyses, such as pith-node counting (Niklasson, 2002) or within-tree-crossdating, also called serial sectioning (Kolishchuk, 1990; DesRochers and Gagnon,

1997; Gutsell and Johnson, 2002; Niklasson, 2002; Bär et al., 2006). Studies have suggested that CMORs are caused either by soil accumulation around the stem or by other limiting environmental factors, e.g. light limitation (Gutsell and Johnson, 2002; Niklasson, 2002). This brings up the question if individual plants growing at their species physiological limit, where adverse growing conditions are expected to be more frequent (Körner, 2003), also show CMORs and whether those are distributed equally between different environments, growth forms and species (broad leaved versus coniferous species). In this study we will explore this question by testing seven tree and six shrub species growing at or near their physiological limits: at high elevations and latitudes, on peatlands and permafrost influenced soils, as well as in semi-arid conditions. Additionally, we introduce and discuss several hypotheses of how the non-formation of growth rings can arise to stimulate further research on this morphological phenomenon.

Materials and methods

Sample sites (Fig. 1, Table 1)

Shrubs at their elevational limit

Denali National Park, Alaska, USA: at three south-facing slopes in and around Denali National Park we sampled six individuals each of *Salix alaxensis* (Andersson) Coville, *Alnus crispa* (Aiton) Pursh and *Juniperus nana* Wild, as well as five individuals of *Betula nana* L. We sampled the individuals of each species at their elevational margin of distribution on south-facing slopes with an inclination of 5–25°. Distance between sampling disks was 20 cm.

Central Europe, Czech Republic: 26 individuals in three stands (8, 11, and 7 individuals respectively) of *Pinus mugo* Turra were sampled in the Giant Mountains (Krkonoše Mountains) close to the border between Poland and the Czech Republic. Individuals grew between the treeline, consisting of *Picea abies* L. at 1350 m above sea level (asl) and the upper limit of the *P. mugo*-distribution at 1470 m asl. *P. mugo* shrubs were sampled by taking penetrating cores with an increment borer with an irregular sampling interval of 37–299 cm. Basal stem parts were typically overgrown by a dense mat of grasses. We sampled a total of 26 individuals

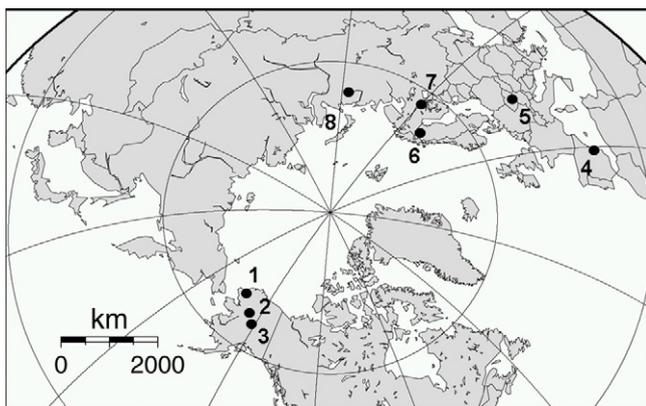


Fig. 1. Map of sampling locations. 1: Noatak River, Alaska, U.S.A. (*Picea glauca*); 2: Interior Alaska, U.S.A. (*Picea mariana*, *Picea glauca*); 3: Denali National Park, Alaska, U.S.A. (*Alnus crispa*, *Betula nana*, *Juniperus nana*, *Salix alaxensis*); 4: Guardamar, SE Spain (*Pinus halepensis*, *Pinus pinea*); 5: Giant mountains, Czech Republic (*Pinus mugo*); 6: Abisko, Sweden (*Betula nana*, *Betula pubescens* Ehrh. ssp. *czerepanovii*, *Juniperus nana*, *Salix glauca*); 7: Salmisuo, Finland (*Pinus sylvestris*); 8: Usa basin, Komi Republic, Russia (*Betula pubescens*, *Picea obovata*).

Table 2

CMORs (continuously missing outer rings) could be found in nine out of 13 species or eleven out of 17 sites. All sites were resource limited and typically represented marginal habitats for the woody plants growing there. On average, 29% of the sampled individuals contained CMORs.

Site specification	Species	# of individuals sampled	Disk (D) or core (C)	# of disks/cores	# of radii	% individuals with CMORs	# of CMORs: min/average/max
Elevational shrubline	<i>A. crispa</i> , Alaska	6	D	31	72	00	0
	<i>B. nana</i> , Alaska	5	D	21	50	00	0
	<i>B. nana</i> , N-Sweden	8	D	43	92	12	14/7/14
	<i>J. nana</i> , Alaska	6	D	48	144	17	5/0.8/5
	<i>J. nana</i> , N-Sweden	33	D	190	365	73	1/10/82
	<i>P. mugo</i> , Czech Republic	26	C	79	158	38	3/11/72
	<i>S. alaxensis</i> , Alaska	6	D	21	56	17	3/0.5/3
	<i>S. glauca</i> , N-Sweden	2	D	10	25	50	1/0.5/1
Elevational treeline	<i>B. pubescens</i> ssp. <i>czerepanovii</i> N-Sweden	81	C	162	324	30	1/1.6/8
	<i>B. pubescens</i> ssp. <i>czerepanovii</i> N-Sweden	6	D	33	66	17	4/0.7/4
Latitudinal treeline	<i>B. pubescens</i> , NW Russia	1	D	9	22	00	0
	<i>P. glauca</i> , Alaska	3	D	14	28	00	0
	<i>P. obovata</i> , NW Russia	3	D	22	64	00	0
Wet hydrological limit	<i>B. pubescens</i> , N-Sweden, mire	5	D	51	123	80	2/6.8/15
	<i>P. sylvestris</i> , Finland	5	D	51	128	80	2/4.8/13
Dry hydrological limit	<i>P. pinea</i> , SE Spain	3	D	21	168	67	2/1.3/2
	<i>P. halepensis</i> , SE Spain	3	D	14	112	67	1/0.6/1
Permafrost influences soils	<i>P. glauca</i>	3	D	9	19	00	0
	<i>P. mariana</i> , Alaska	19	D	41	67	00	0
Total amount/average		212	–	615	2055	29	0/3.7/82

North Sweden: at a south slope in the Abisko valley (N 68°21', E 18°41'), 33 individuals of *Juniperus nana* (Willd.), eight individuals of *Betula nana* L. and two individuals of *Salix glauca* L. were collected in an elevational belt stretching from treeline (700 m asl) to the upper limit of the *Juniperus* distribution at 1100 m asl. The vegetation surrounding the shrub patches mainly consisted of dwarf shrub tundra or subalpine meadow communities. Only shrubs without apparent signs of competition, herbivory, or ground disturbance were sampled. The sampling interval between the serial stem disks was 10 cm.

Trees at their elevational limit

North Sweden: six *Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti individuals with monocormic growth form were sampled at the elevational treeline at the north side of Lake Torneträsk. Six stem disks per tree were sampled at defined stem heights (5 cm, 25 cm, 50 cm, 90 cm, 140 cm and 200 cm). In addition, we sampled 81 *Betula* individuals with a less destructive sampling design by coring each tree at two different height levels with an increment borer. Samples were retrieved from two transects on mountain slopes east and west (westerly, respectively easterly exposure) of Lake Torneträsk. *Betula* trees in some parts of the area had suffered substantially from an outbreak of the autumnal moth (*Epirrita autumnata* Bkh.) causing defoliation of the tree crowns in 2004 (see Babst et al., 2010 for methodology, disturbance distribution and intensity). In addition, 16 trees of those that had died because of the moth infestation were sampled on the east side of the lake, at the elevational margin of the *Betula* population.

Trees at their latitudinal limit

Noatak, NW Alaska: northern treeline in Alaska is formed by *Picea glauca* (Moench) Voss. We sampled three individuals from an advancing treeline in north-west Alaska, above Noatak Canyon.

There, trees are advancing into gently rolling upland tundra. Distance between sampling disks was 25 or 50 cm respectively.

NW Russia: samples from *Picea obovata* L. were taken from trees growing beyond the current northern treeline formed by the same species (at N 67°22', E 62°11'). The terrain was mainly flat and mostly underlain by permafrost. The sampled trees, however, most likely grew in permafrost free soil pockets, as *P. obovata* has difficulty growing on permafrost (Virtanen et al., 2004). Distance between sampling disks was 50 cm, starting at the root collar.

One *B. pubescens* individual was sampled several hundred meters north of the northernmost *Picea* stand in the region at a well drained and wind protected site at a river bluff. There, five *Betula* individuals grew widely spaced without apparent competition. Distance between sampling disks was 50 cm.

Trees at their wet hydrological limit

Eastern Finland: we sampled eight stunted *Pinus sylvestris* trees growing mostly on top of small hummocks in the Salmisuo peatland, an oligotrophic mire complex (Becker et al., 2008). Trees were sampled by complete extraction including the main root system and sectioned with a sampling interval between 5 and 30 cm, with a minimum of five sections per individual.

North Sweden: five individuals of *B. pubescens* (Ehrh. ssp. *czerepanovii*) (Orlova) Hämet-Ahti were sampled in an oligotrophic peatland about 2 km west of Abisko village. The *Betula* trees were growing on small hummocks of *Sphagnum* mosses. Distance between sampling disks was 50 cm.

Trees at their dry hydrological limit

SE Spain: three individuals of both, Aleppo pine (*Pinus halepensis* Mill.) and Stone pine (*Pinus pinea* L.) were sampled, growing in a mixed even-aged pine forest on the south-east coast of Spain (Guardamar del Segura, 38° 6'N, 0°40'W). The trees were planted there at the beginning of the 20th century as protection against

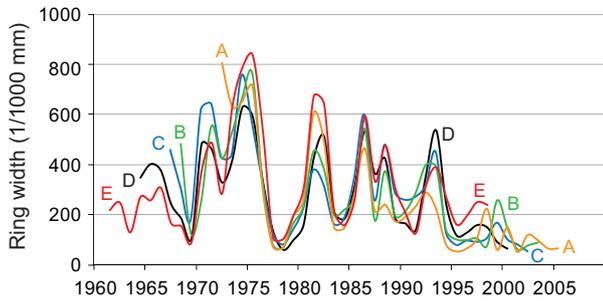


Fig. 2. Example for successful crossdating of several height levels of one individual tree (*Pinus sylvestris* from a Finnish peatland) collected at heights of –24 cm (E), –14 cm (D), –5 cm (C), 0 cm (B) and +5 cm (A). At the lowest disk (E) growth started in 1961 and no rings have formed since 1999, whereas at level (A) growth started in 1972 and rings have formed until the year 2005 when the tree was sampled.

sand dune movement. The climate at this study site is thermo-Mediterranean and semiarid. Trees without visible damages and anomalies were felled and dissected at the base (0.33 m), at breast height (1.4 m) and then with a distance of approximately 1 m between the sampling disks up until the tree top (Novak et al., 2011).

Trees on permafrost influenced soils

Interior Alaska: the trees sampled were growing along the Yukon River on permafrost influenced soils. 19 *Picea mariana* (Mill.) Britt., E.E. Sterns & Poggenburg and three *Picea glauca* individuals were sampled by felling and dissection at stem base, at 6 m height and at the crown level (2–3 sections per individual).

Sample preparation

In most cases, the root collar was located in the field (in some cases by digging) and extracted with the whole stem(s). Large trees were cut as low as possible. Where applicable, one main stem per shrub and polycormic tree and the whole stem of each monocormic tree were dissected (Table 2). Where the dissection of the whole plant was not feasible due to practical or conservational concerns, trees (*B. pubescens* in Sweden) or shrubs (*P. mugo*) were cored at different stem height levels. Disks or cores were labeled according to their former position on the stem and sanded with sand papers of progressively finer grit size (80, 180, 240 or 300, 500, 800) until growth ring structures were clearly visible. If this procedure did not produce surfaces sufficient for ring boundary detection, we thin-sectioned the sample (*B. nana*, some *P. sylvestris*). The resulting wood slices were between 10 and 20 μm thick. Thin-sections were transferred onto microscope slides, stained with a mixture of Safranin and Astrablue to increase contrast and then sealed with Euparal under a cover glass.

Ring width measurements and the serial sectioning technique

On each stem disk (height level), core or thin-section, ring widths of two to eight radii were measured with an accuracy of 0.01–0.001 mm (LINTAB 5 and TSAPWin, Rinntech, Heidelberg) depending on the sampled species. Normally, between six and 24 radii (minimum 4, maximum 72) per individual plant were measured. First, all radii of one disk (height level) or the two radii of one core were crossdated, compared, remeasured if necessary, and finally averaged. Only a few radii, notably some close to the tip of the shrub stems (usually those with less than 25 growth rings) had to be excluded from further analysis, because they could not be crossdated.

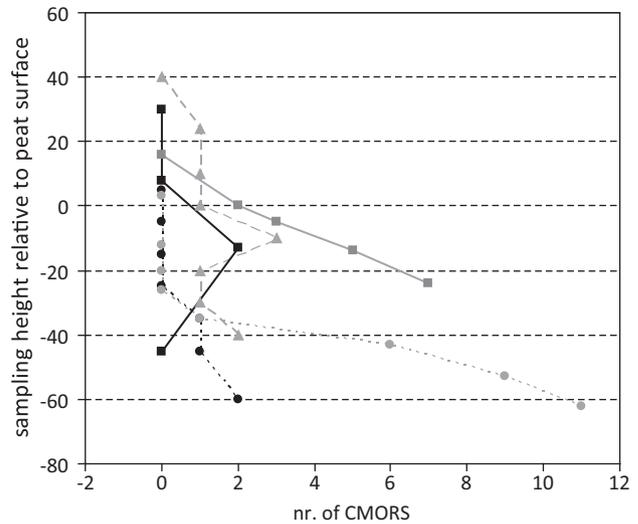


Fig. 3. Five *Pinus sylvestris* trees from a peatland in Salmisuo, Finland. Number of CMORs (x-axis) increases with depth of peat (here y-axis). 0 cm refers to the peat surface at sampling time (2005). Please note that each tree established at the peat surface and that peat accumulated in the following years, subsequently embedding the stem.

Then all disks (height levels), cores or thin sections of each individual plant were crossdated, using the serial sectioning method (Kolisshchuk, 1990). Basically, the serial sectioning method treats all samples within a stem as successively “floating”. The method assumes that the samples from higher up on the plant are more likely to show the last growth rings while samples from lower stem portions might have CMORs (last years of growth). The successive overlap of the separate tree-ring series of each height level from the top to the basal part of the stem insured the correct assignment of each sample (radius) to the period in time, when growth had actually occurred (Fig. 2). In the case of the 81 *B. pubescens* ssp. *czerepanovii* trees from the elevational treeline in Sweden, we analyzed missing rings and CMORS by crossdating between all individuals and also compared them with a *B. pubescens* and *P. sylvestris* chronology from the area (Van Bogaert et al., 2009; Babst et al., 2010).

Results

In total, 202 individuals (92 shrubs and 110 trees) were sampled (Fig. 1, Table 1) and ~20% of all sampled individuals showed CMORs. Within a single species, the proportion of individuals with CMORs ranged from 0 to 80%. The number of CMORs within an individual generally decreased with increasing sampling height on the stem (e.g. Fig. 3). CMORs occurred in the genera of *Betula* (shrubs and trees), *Juniperus*, *Salix* and *Pinus* (shrubs and trees), but not in *Alnus* and *Picea*. In the following, we will present the results of each species near its distributional or local physiological limit.

Shrubs at their elevational limit

Alnus crispa (Alaska, n=6): ring boundaries were clearly visible after sanding. None of the individuals from the elevational shrubline in central Alaska did show any CMORs. The age of the individuals ranged between 25 and 68 years.

Betula nana (Alaska, n=5; Sweden n=8): ring boundaries were very faint and therefore hard to distinguish so that all samples were thin-sectioned. Frost rings occurred infrequently. The Swedish samples showed a high percentage of wedging rings. LMRs within but even more between the different stem disks of one

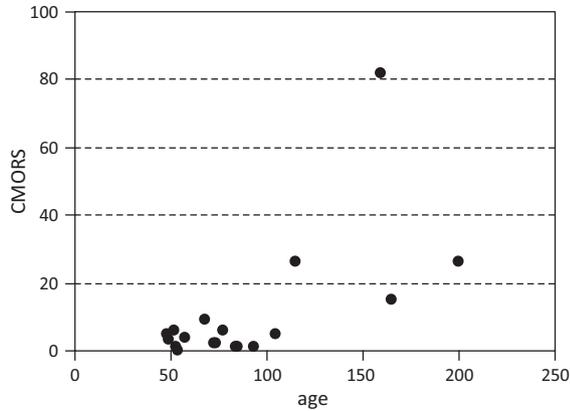


Fig. 4. Age (x-axis) of *Juniperus nana* individuals from Sweden correlated positively with the number of missing outer rings at stem base (CMORs; y-axis). All individuals more than 100 years old have CMORs, while younger individuals do not show a general trend.

individual were the rule. Due to low synchronicity within the individuals, seven individuals had to be rejected from further analysis for this study. One individual from Sweden had CMORs; but no CMORs occurred in the samples from Alaska. The individuals from Alaska had a more erect growth form with a lot of branches, whereas the samples from Sweden were dwarfed and often grew in a prostrate cushion close to the ground. The mean age of the Swedish samples was 53 years compared to 34 years for the samples from Alaska, and the oldest individuals were respectively 71 and 51 years old.

Juniperus nana (Alaska, $n=6$; Sweden $n=33$): ring boundaries were clearly distinctive. However, sometimes strong eccentricity, wedging rings and the occurrence of compression wood made it difficult to age and crossdate samples, often requiring more than two measured radii per stem disk. In Sweden, out of 33 individuals, 24 individuals (73%) had CMORs. In one individual, 82 missing rings at a stem height of 10 cm (the total stem length was 450 cm) were recorded. The number of missing rings was related to the age of the shrub specimen (Spearman correlation $r=0.58$, $P<0.001$; Fig. 4). In Alaska, we analyzed six individuals, one had CMORs. *Juniperus nana* from Sweden reached ages up to 174 years in living individuals and 323 years in a sub-fossil individual; the samples from Alaska were between 50 and 149 years old.

Pinus mugo (Czech Rep., $n=26$): ring boundaries were clearly visible after sanding. Wedging rings occurred infrequently and compression wood occurred mostly only in the upper part of stems. In two of the three different pine stands investigated, 57% respectively 87% of all individuals had missing outer rings. For these two stands the number of missing years at the stem base varied from 3 to 72 and showed a significant positive relationship with stem length (Spearman correlation $r=0.57$, $P=0.013$, Fig. 5). The mean age of all individuals was 117 years.

The third *Pinus mugo* stand (11 individuals) had been heavily infested in the 1940s by the diptera species *Thecodiplosius brachynytera* Schwägrichen, a gall midge that reduces needle production. In most cases, radial growth had ceased completely apart from the uppermost parts of the branches in the year 1940 and the following decade. In some cases, growth had not resumed until 1958 (Fig. 6). Despite of up to 18 years of stagnation, growth resumed in all parts of the stems and subsequent CMORs were only observed in one individual of the stand from 2000 to 2003.

Salix alaxensis (Alaska, $n=6$): ring boundaries were clearly visible after sanding. However, all individuals of this species had been attacked by wood decaying fungi. CMORs occurred in one of the six individuals that were sampled. This plant was the oldest (48 years)

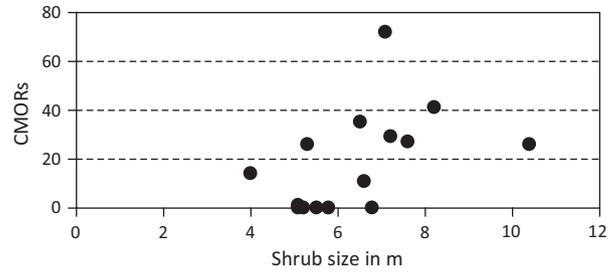


Fig. 5. Shrub size (stem length in m) of *Pinus mugo* individuals from the treeline of the Giant Mountains in the Czech Republic correlated positively with the number of missing outer rings at stem base (CMORs; y-axis).

and showed the severest damage caused by these fungi. Half of the plant's cambium had been destroyed along the whole stem length at the time of sampling. The mean age of the sampled individuals was 32 years.

Salix glauca (Sweden, $n=2$): due to growth rings with a width of only one or a few cell rows, samples of *Salix glauca* had to be cut with a razorblade after sanding and treated with chalk dust to make all rings visible. Despite the occurrence of wedging rings, radii of different disks had a comparably high synchronicity. Continuously missing outer rings occurred in one of the two individuals sampled. The individuals were 39 and 42 years old.

Tree species at their elevational limit

Betula pubescens ssp. *czerepanovii* (Sweden, $n=87$): growth rings of *Betula* were visible after sanding, but sometimes difficult to distinguish due to the diffuse-porous wood structure. Wedging rings were common in all samples.

From the six stands (81 living trees) that were cored (Table 2), four stands had trees with CMORs at the stem base (24 living trees total). The proportion of trees with CMORs varied according to the degree of defoliation caused by an outbreak of the autumnal moth (*Epirrita autumnata* Bkh.) in the year 2004 (Fig. 7). Neither the undamaged nor the moderately damaged stand had any trees with CMORs, but the heavily damaged stands had between 25 and 80% of trees showing CMORs at stem base. In one severely affected stand, 16 trees had died shortly after the moth outbreak. From the six *Betula* samples that were completely dissected, CMORs only occurred in the oldest individual (148 years). The mean age of all birch trees was 74 years.

Tree species at their latitudinal limit

B. pubescens (NW-Russia, $n=1$): only one *Betula* tree was sampled, a single tree north of the latitudinal treeline formed by *P. obovata*. Ring boundaries were distinctive and, despite one LMR, neither wedging nor continuously missing outer rings occurred in this 53-year old sample.

Picea obovata (NW-Russia, $n=3$): growth rings of *P. obovata* were generally distinctive. Wedging rings that were usually associated with strong compression wood formation (with changing radial direction) regularly occurred in all sampled trees. The synchronicity of all series within each tree was very high. No LMRs were observed and none of the sampled trees showed any CMORs. The oldest individual was 162 years old, the youngest 107 years.

Picea glauca (Alaska, $n=3$): growth rings were distinctive and eccentric growth existed. The sampled individuals at this advancing treeline had a mean age of 64 years. Synchronicity of all series within each tree was very high. No locally missing rings were observed and none of the sampled trees showed any CMORs.

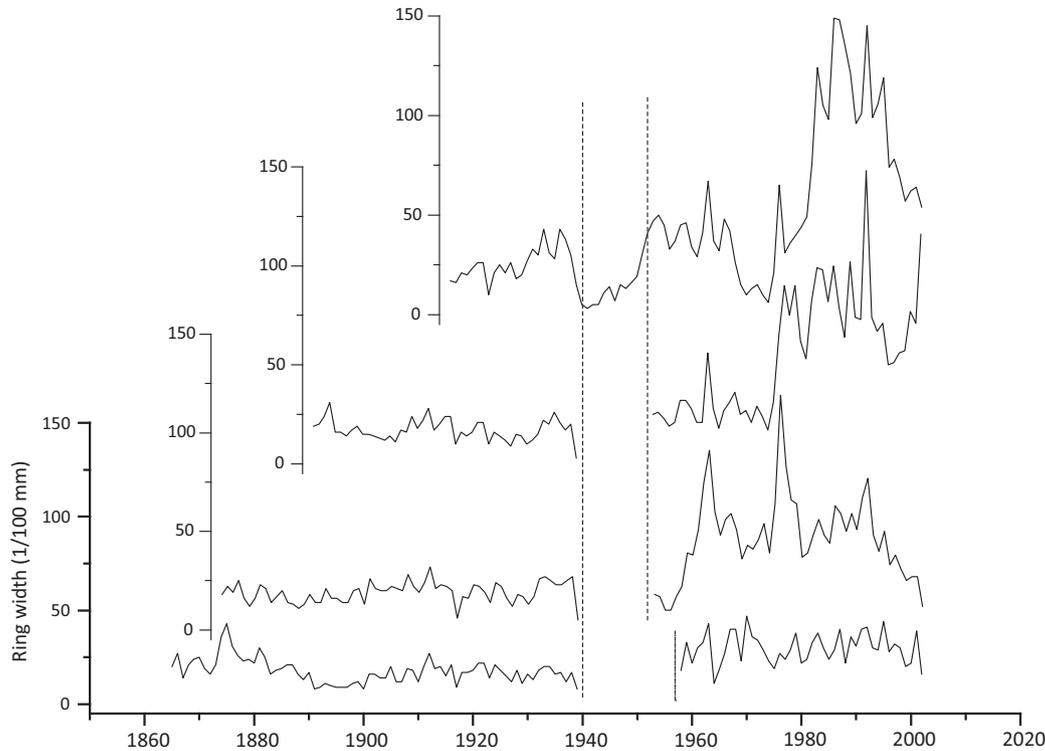


Fig. 6. Four height levels of a 137 year old *Pinus mugo* individual from Central Europe in a stand heavily invested by a diptera species (*Thecodiplosius brachyntera*) in 1939. In that year slow growth (0.08 mm on average) still occurred in all height levels (height levels in ascending order at 86, 100, 128 and 165 cm height from stem base; total shrub size 300 cm). From 1940 onwards, no wood production occurred for 18 years (lowermost level), respectively for 13 years in the two height levels above. The shrub however still produced very narrow annual rings at its top half (highest level, > 165 cm).

Tree species at their wet hydrological limit

B. pubescens ssp. *czerepanovii* (Sweden, n=5): growth rings of *Betula* were distinctive after sanding and preparing the surface with razorblades and chalk. Often, three to five radii of each disk had to be measured because of a lot of wedging rings. Also, up to five locally missing rings occurred. Ages ranged from 61 to 160 years with a mean age of 68 years. Four out of five individuals (80%) had CMORs both at lower and higher stem height, with slightly more rings missing at the base of the stem. Even in the single individual that had no missing rings at the stem base, the outermost ring was missing in the middle and the top part of the stem. The heartwood

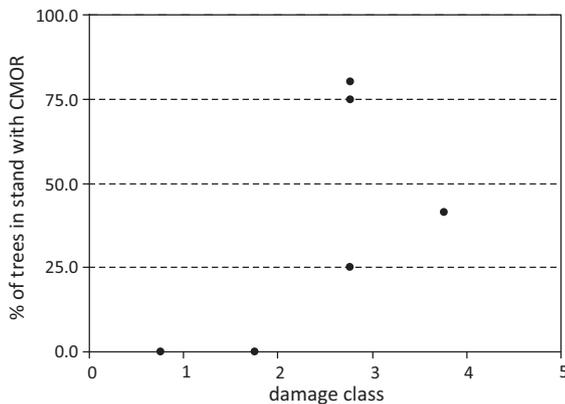


Fig. 7. Percentage of *Betula* individuals showing CMORs at six different sites increased with increasing defoliation intensity during the 2004 outbreak of *Epirrita autumnata* in the area of Lake Torneträsk, Sweden. The damage classes were derived from a digital change detection method applied to Landsat TM/ETM+ Normalized Difference Vegetation Index (NDVI) images (Babst et al., 2010).

of the oldest individual was rotten and the foliage of all trees was scarce.

Pinus sylvestris (Finland, n=8): ring boundaries were clearly visible and very distinctive. Wedging rings occurred frequently, compression wood was seen in all samples. The root collar was located between 60 and 24 cm below the peat surface (Fig. 3), because the lower stem sections of the trees that originally had established at the peat surface during germination were thereafter successively encased by growing layers of peat. From the eight pines sampled, the three youngest, all less than 45 years old, could not be cross-dated and were excluded from further analysis. Four out of the five remaining samples showed CMORs (Fig. 3). The part of the stem where CMORs occurred was nearly always below the present peat level and adventitious roots had formed in some cases below the peat surface. In two individuals, CMORs were also found in sections of the stem above the peat surface. Tree age ranged from 34 to 98 years and the number of CMORs was not related to age but the height levels of the sampled disks in relation to the present peat surface correlated significantly and negatively with the amount of CMORs (Spearman correlation $r = -0.47$, $P = 0.04$), i.e. the deeper the root collar was situated below the peat surface the more CMORs occurred (Fig. 3).

Tree species at their dry hydrological limit

Pinus halepensis and *Pinus pinea* (Spain, n= 3 each): locally missing rings (LMRs) occurred in 61% of the analyzed years in *Pinus halepensis* and in 24% of the analyzed years in *Pinus pinea*. In both species, the frequency of LMRs has increased in the last few decades (Novak et al., 2011). The comparison of different stem height levels showed that the frequency of LMR gradually decreased from the lower to the upper part of all *P. halepensis* trees ($P < 0.05$). To the

contrary, no significant relationship was established for *P. pinea* trees. CMORs occurred in four samples (PIHA 1 in 1995, PIHA 2 in 1995, PIPN 1 in 1995 and 2001, PIPN 2 in 1995 and 1999) from the ground level to above breast height (Novak et al., 2011).

Tree species on permafrost influenced soil

Picea mariana ($n=19$) and *Picea glauca* ($n=3$) (Alaska): the growth rings of this species were distinctive and eccentric tree growth existed. The sampled individuals at the two sites had a mean age of 137 and 197 years, respectively. Synchronicity of all growth ring curves among the two to three sampled height levels within each tree was very high. Nearly no locally missing rings (LMRs) were observed and none of the sampled trees showed any CMORs.

Discussion

Generally, the occurrence of a successively increasing number of missing outer rings within the lower portion of the stems (CMORs) of several shrub and tree species is surprising, since it is generally assumed that woody plants growing in a seasonal climate form every year a ring extending from the tip of the branches to the root collar. Even though our sample size varied a lot (ranging from a single individual to 81 individuals of a species) we found CMORs both in angiosperms and gymnosperms, and both in shrubs and trees. Of the 13 sampled species, only five did not show CMORs. However, we assume that a larger sample size and the inclusion of other types and conditions of environments (e.g. a retreating treeline) would have resulted in an even higher proportion of species with CMORs. Our results suggest that CMORs are a general strategy of woody plants to deal with extreme environmental conditions and that they might favorably occur in prostrate growth forms, where structural support is of less importance than for upright growth forms such as monocormic trees and therefore annual radial growth along the whole stem might not be necessary.

To gain a better understanding of the processes leading to the (non-)formation of growth rings, it is useful to briefly recapitulate the physiological processes leading to radial growth. In simplified terms, at the beginning of the growing season, when buds break, auxin or indole-3-acetic acid (IAA) is produced in the apical meristem and transported actively downward in the stem, with additional influence of gravity; (Forest et al., 2006). IAA triggers the cambium to become active and to start xylogenesis. This process is dependent on (i) the concentration of IAA per unit area in the cambium: i.e. the more the IAA, the higher the rate of xylem production (Tuominen et al., 1997; Ugglä et al., 1998; Kramer, 2001), (ii) the temperature regime in the stem (Begum et al., 2008), and (iii) the availability of "resources" such as water, sugars and cellulose. The individual thus needs a functioning canopy and root system. In addition, other factors might play a role in the formation of new cells such as the age of the cambium (Rossi et al., 2008).

For the start of the earlywood formation and the formation of a detectable growth ring, each of these physiological processes has to be functional and certain environmental conditions have to be met. If one of these prerequisites is not met, no radial growth will occur at specific places within the stem (LMR) or along the entire length of the stem (CMORs). In the following, we will briefly discuss the possible influences of each of these factors on the non-formation of growth rings.

Auxin (IAA)

Since continuously missing outer rings (CMORs) occur mainly at lower stem portions, IAA (produced in the apical meristem)

transport speed might play a role in the non-formation of growth rings. Growing seasons in arctic or alpine regions can be very short and low stem temperatures might additionally slow down transport speed. Published values of IAA transport speed range from 2 to 15 mm/h (Hussey and Gregory, 1954; Morris, 1979), but none of these studies was carried out at individuals at their physiological growth limit and we can thus assume IAA transport speeds in most of our sampled individuals to be at the lower end of the spectrum or even below. However, even if we assume transport speeds of around 1–2 mm/h, it would take around one to two weeks for IAA to reach the lower portions of a 3 m tall (or long) individual (e.g. a *P. sylvestris* or *J. nana* stem). Therefore, it is unlikely that IAA transport speed alone accounts for the observed CMORs in our samples.

Several other facts argue against a direct link between IAA deficiency and CMORs: (i) In some species, such as *P. sylvestris*, IAA can be stored locally over the dormant season (Egierszdorff, 1981) or be synthesized to some degree in the stem (Sundberg and Ugglä, 1998; Kramer, 2001) and made available to activate cambial activity even before the newly formed IAA reaches lower stem portions. (ii) Every individual needs to produce new fine roots during every season to acquire nutrients and root growth depends on IAA formed in the apical meristem (as well as on IAA formed in situ). This implies that at least some IAA needs to be transported to the root system bypassing the zone of stopped cambial activity (CMORs). It is therefore unlikely that the reason for cambial inactivity in the lower stem portions of individuals showing CMORs is a simple IAA deficiency.

On the other hand, there was a significant positive correlation ($r=0.47$, $P=0.036$) between stem length and CMORs in two stands of *P. mugo* ($R^2=0.23$; Fig. 5). In combination with other factors affecting cambial activity and cell formation processes, such as temperature within the stem and age of the plant, non-functioning or slowed IAA transport could still cause a delayed cambial activity in the basal areas of the stem and a subsequent lack of ring formation there.

Temperature

Temperature highly affects plant processes and is as such closely linked to both IAA production and transport, and to cambial activity. Since IAA is actively transported, we would expect temperature to have a significant effect on transportation rates, slowing down or effectively stopping transport at very low or high temperatures. Cooling or warming of stem portions of *P. abies* resulted in reduced respectively enhanced cambial activity (Gričar et al., 2007), measured by the number of cells formed during the treatment. Under natural conditions, temperature seems to be the main factor controlling initial divisions in the xylem and in the radial cell expansion in *Larix sibirica* Ledeb. and *P. sylvestris* (Antonova and Stasova, 1997; Gruber et al., 2010). In general, optimum functions (Antonova and Stasova, 1997) and threshold effects (Rossi et al., 2007, 2008) characterize the relationship between temperature and the onset of xylem differentiation. Critical temperature values for the differentiation of xylem cells of conifers in cold climates seem to converge around 5–9 °C (Rossi et al., 2007, 2008). Even though daily temperatures below these values are still favorable for photosynthesis, they could inhibit the allocation of assimilated carbon into structural investment, i.e. xylem growth (Rossi et al., 2008) and thereby growth ring formation.

In our samples, shrub or tree stems that were in contact with the ground surface and were partly overgrown by soil or encased in peat should not have been as exposed to diurnal temperature fluctuations as woody plants with an erect growth form. However, because soil temperatures are likely to be lower than the surface- and air-temperatures affecting the upper part of the plant, the onset of the cambial activity at the stem base may have been delayed.

This might also apply for woody plants growing on permafrost; however, our sampled *P. mariana* trees from Alaska did not show any CMORs. In *P. abies* and *P. cembra* individuals growing at tree-line in the Alps, cell tissue in the basal parts of stems was frozen four times longer than in the upper parts, causing cambium activity to be decoupled within one stem (Mayr et al., 2006). A reduction of the growing season length in the lowermost parts of the plant stems could be a possible factor explaining the increasing number of CMORs with decreasing sampling height on the stem as observed in all our samples.

Resources

In addition to a favorable temperature regime and the presence of hormones initiating cambial activity, “resources” such as water, nutrients and carbohydrates need to be available for the formation of new cells. In some cases, a lack of resources might be the reason for a reduction of radial growth in certain stem portions. Insect outbreaks and subsequent defoliation may cause reduced radial growth or even a complete growth inhibition for several years. In northern Sweden, *Betula* trees in stands that had experienced more severe defoliation as compared to other stands also showed more CMORs (Fig. 7). For *B. pubescens*, strong decreases of ring-width following severe defoliation have been reported (Hoogesteger and Karlsson, 1992). The same could be true in our case, where only the strongly defoliated stands showed CMORs. As observed in our samples of *P. mugo* from Central Europe that suffered from an insect attack, cambial division can resume even after more than a decade of inactivity at the stem base if the upper stem part stays alive and growth can continue after recuperation of the canopy (Fig. 6). Ring formation after recuperation reached pre-defoliation levels and the individuals were able to survive this extended period of stress without any visible long-term damages, such as subsequent reduced growth or structural anomalies. This suggests that woody plants at their range margin, in extreme environments or under adverse growing conditions can have very plastic resource allocation patterns. The cambium of such plants may be inactive at the stem base, yet resume vital for many years.

Resource deficiency may also explain the occurrence of CMORs observed in four of our samples from the semi-arid site in Spain. Due to water deficiency (drought) and subsequent stomata closure, photosynthetic rates typically drop and fewer carbohydrates are available for radial growth (McDowell et al., 2008). Since radial growth starts at the top of the plant, not enough resources seem to have been available for cytogenesis in the basal stem area of the two pine species (*P. halepensis*, *P. pinea*) in the years with no wood formation at the stem base. In addition, both sampled species at this site showed a high frequency of LMRs and even TMRs, especially in recent years (Novak et al., 2011). While LMRs occurred at each height level, they were more likely to occur in lower stem portions of *P. halepensis*, but not in *P. pinea*. LMRs seem to be the first indication that an individual is under stress. If stress levels increase, LMRs seem to occur at more height levels. If stress levels continue to increase and other factors that favor the non-formation of wood, such as tree height (Novak et al., 2011) come into play, CMORs might be the result.

Influence of cambial age

The age of woody plants has been identified as one factor possibly influencing timing and duration of xylogenesis. For example, in three conifer species growing at treeline in the Alps, the onset of cell production in older individuals in comparison with younger individuals at the same sites was delayed and the total duration of cambial activity shortened by two to three weeks (Rossi et al.,

2008). However, it is difficult to distinguish age from size effects: at the end of winter, larger stems with thicker bark remain colder for longer periods (Mayr et al., 2006), thereby shifting the start of temperature-dependent xylogenesis back in time (see “Temperature” section). The resulting shorter period of cambial activity in larger and/or older individuals might be a factor contributing to the observed CMORs in this study. We found evidence for the influence of both parameters (age and size) in our dataset: we observed a significant positive correlation between individual ages and the number of CMORs in *J. nana* as well as a significant positive relationship between stem length and CMORs in *P. mugo* (Figs. 4 and 5).

Influence of growth form

For polycormic individuals, an additional factor needs to be considered. Since we only sampled one stem of the multiple stems belonging to each individual, we do not know if lower portions of the other stems possibly had formed the growth rings that were missing in our sample. It is thus possible that the individual plant might have allocated growth resources selectively to only some stems of the plant, even though the underlying physiological processes for this mechanism are unclear. However, the fact that it was possible to successfully crossdate (a) different height levels of the sampled main stems and (b) different individuals shows that the allocation of resources cannot occur completely random within single plants, as the upper parts of the sampled stems showing CMORs did grow in these specific years.

The fact that the circumference of some shrub stems stays the same over large portions of these stems (as opposed to cone-shaped tree stems) also suggests a lower investment of resources into radial growth in the lower stem portions, making the occurrence of CMORs more likely. The stunted and twisted growth form of some shrubs, especially at elevational shrublines, reduces the need for a thick lower stem, since it maximizes canopy area sideways, reduces wind exposure and thus also structural requirements. While this observation remains hypothetical, it does fit well with our observations of high numbers of CMORs in species following this general growth pattern (i.e. *J. nana* or *P. mugo*). This hypothesis is further supported by the fact that CMORs in *B. nana* only occurred in one Swedish sample, an individual that grew close to the ground surface in contrast to the more erect samples from Alaska showing no CMORs.

Finally, many trees and shrubs in our sample set were growing at their absolute distributional limit; either regionally (e.g. at high elevation) or locally (e.g. on peatlands). Often these individuals had a poor canopy, both in size and foliage area, relative to their stem size. This observation could be an additional factor affecting the supply of “resources” for radial growth. The canopy size might simply not be sufficient to produce enough carbohydrates for the formation of a new growth ring along the whole length of the stem. This hypothesis would be a logical extension of the well known fact that increased shading or reduced canopy size reduces stem wood production in forest trees (Schweingruber, 1996).

Combined factors

Altogether, none of the factors mentioned alone seems to be able to sufficiently explain the occurrence of CMORs in such a diverse array of species and environments. Under different environmental conditions different factors can influence the formation of wood negatively and most likely, several factors act interlinked to produce CMORs. For example in some of the older *Juniperus* samples high cambial age co-occurs with colder microsite conditions close to the ground and a sparse canopy relative to the length of the stem. Therefore it seems that radial growth of woody plants under

accumulated stress is controlled by environmental factors acting differently on different parts of the individual. Also, internal regulatory mechanisms such as IAA, activating xylogenesis, or cambial age likely play an important role by selectively activating cambial regions and preferentially investing resources in upper stem parts with the cost of reduced or halted radial growth in the lower stem portions.

Conclusion

We found CMORs in about 20% of our sampled 202 individuals and in eight of 13 species. Sampled woody plants had a wide variety of growth forms and species and they came from very different landscapes and micro-topographic and climatic settings. Their common feature was that all specimens were growing near or at the margins of their distribution and were obviously affected by unfavorable growing conditions, some even suffering additional stress from herbivory. Therefore, we conclude that CMORs are neither restricted to certain (prostrate) growth forms nor to a single type of marginal environment. However, some environmental settings seemed to increase the chances of a woody plant to have CMORs, since the highest percentages of CMORs were consistently observed in trees growing on peatlands and in coniferous shrubs at high elevations. It remains to be seen, whether an increased sample size would lead to the discovery of CMORs in the species that did not show CMORs in our study. Some species (e.g. *Picea* sp., *A. crispa*) might just have different physiological mechanisms leading to a continuous xylogenesis all along the stem. At this point, we would recommend the use of the serial sectioning technique for all woody plants growing in unfavorable environments to avoid miss-dating, particularly in the case of low sample numbers and in the absence of an established ring width chronology as verification for the crossdating process.

According to our findings, the cambium as the key element for xylogenesis can be inactive for several years or even decades and then become active again. The cambial response to stress thus might be much more flexible than previously assumed. The cambium can be inactive in small parts of the stem or in the whole stem or only at the stem base. Pinning experiments performed on trees and shrubs growing under extreme conditions covering the whole length of the stem could provide better insights into the phenomenon of CMORs concerning hormone transport and cambial activity. Cooling and heating experiments on the stems of such woody plants could help to gain more knowledge about the influence of temperatures for xylogenesis, and dendrochronological studies of whole individuals could help to disentangle resource allocation patterns in prostrate and erect woody plants.

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