The effects of drought on wood formation

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The leading hypothesis

Environmental information is permanently registered in the tree-ring structure

The relationship between the seasonal dynamics of xylem formation and environmental factors

↓

Estimation of the influence of anticipated climate change scenarios on

tree performance,

wood structure and

adjustment to future weather conditions.

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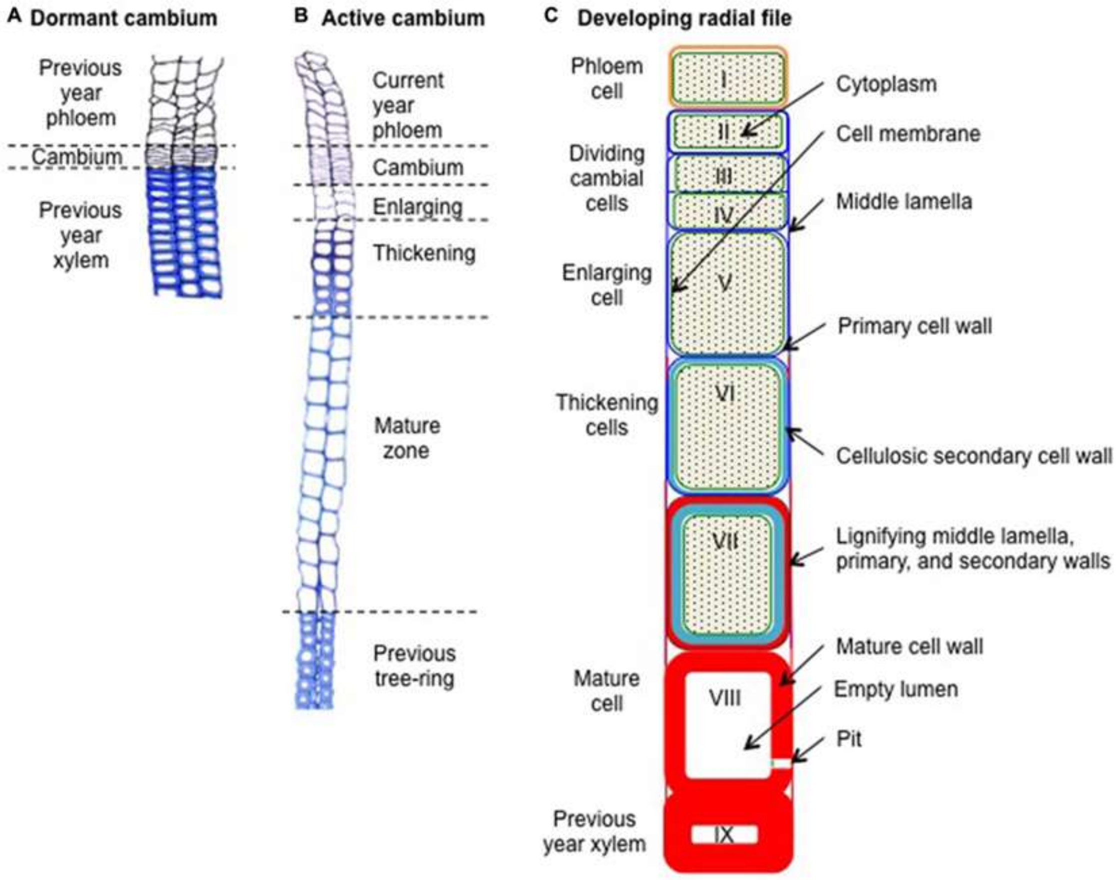
Phenological phases

The radial stem growth is a complex process which includes cell division, cell expansion, cell wall thickening, lignification and programmed death.



The formation of a xylem element can be divided in five major steps:

1. periclinal division of a cambial mother cell that creates a new daughter cell;
2. enlargement of the newly formed xylem cell;
3. deposition of cellulose and hemi-cellulose to build the secondary cell wall;
4. impregnation of the cell walls with lignin; and finally,
5. programmed cell death

Rathgeber CBK, Cuny HE and Fonti P (2016) Biological Basis of Tree-Ring Formation: A Crash Course. Front. Plant Sci. 7:734. doi: 10.3389/fpls.2016.00734

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Scientific Background

- Anatomical features of water-conducting cells have been shown to be reliable ecological indicators, reflecting environmental information different from that stored in tree-ring widths.

- For example, the final size of the water conductive cells (i. e., vessels) can provide information on the environmental conditions that prevailed before and during their formation.

- Vessel features (diameter and vessel area) reflect the relationship between water availability and cell growth.

- Soil moisture content (SMC) may be considered to be a critical factor affecting vessel formation and expansion, while being under turgor pressure control.

Example of conducted research

Title:

The effects of drought on wood formation in *Fagus sylvatica* during two contrasting years.

BRILL

IAWA Journal 37 (2), 2016: 332–348

iawa

THE EFFECTS OF DROUGHT ON WOOD FORMATION IN *FAGUS SYLVATICA* DURING TWO CONTRASTING YEARS

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ABSTRACT

We studied the effect of local weather conditions on intra-annual wood formation dynamics and wood structure of European beech (*Fagus sylvatica* L.) from a temperate location in the Czech Republic in two consecutive years, 2010 and 2011, characterized by different amounts of precipitation. Microcores were taken

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Aim of the Study

- Comparison of the seasonal cambium dynamics and differentiation phases, between two successive growing seasons (2010–2011)

- Detection of the influence of certain environmental factors dominating during growing periods

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Methodology

Sampling

49°28'2.977"N, 16°41'18.131"E,
630 a. s. l.

- Rajec-Domanka research plot
2.5 km north of the Rajec-Nemcice

- 6 sound 130year-old European beech trees
(from 32 - 41 cm in diameter and 32 - 37 m in height)

- Measured Parameters:
  Air temperature
  Precipitation
  Soil Moisture content

- Sampling at weekly intervals (March to October)

- Trephor tool (1.8 mm in diameter)

- Microcores at breast height following a spiral up the trunk

- FAA (formalin-alcohol-acetic acid)

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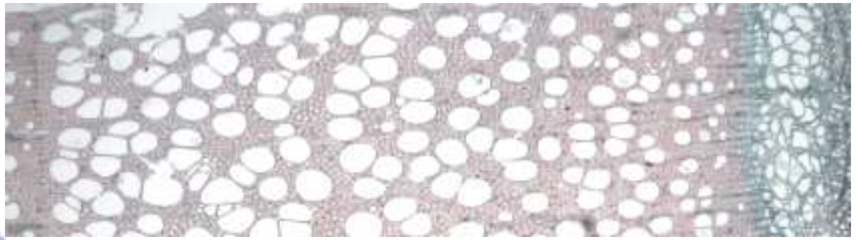
Methodology

Sample preparation

- Dehydration in ethanol series (70%, 90%, 95%, and 100%), and embedding in paraffin
- Cross sections (12 µm thick), cut with a Leica RM2235 rotary microtome.
- Removal of the paraffin (bioclear)
- Staining with a safranin (0.04%) and astrablue (0.15%) water mixture
- Transfer to an object glass (permanent samples)







The observations and histometrical analyses were performed with a Leica DM 2000 microscope (Leica DFC 295 digital camera/ image processing software program ImageJ).

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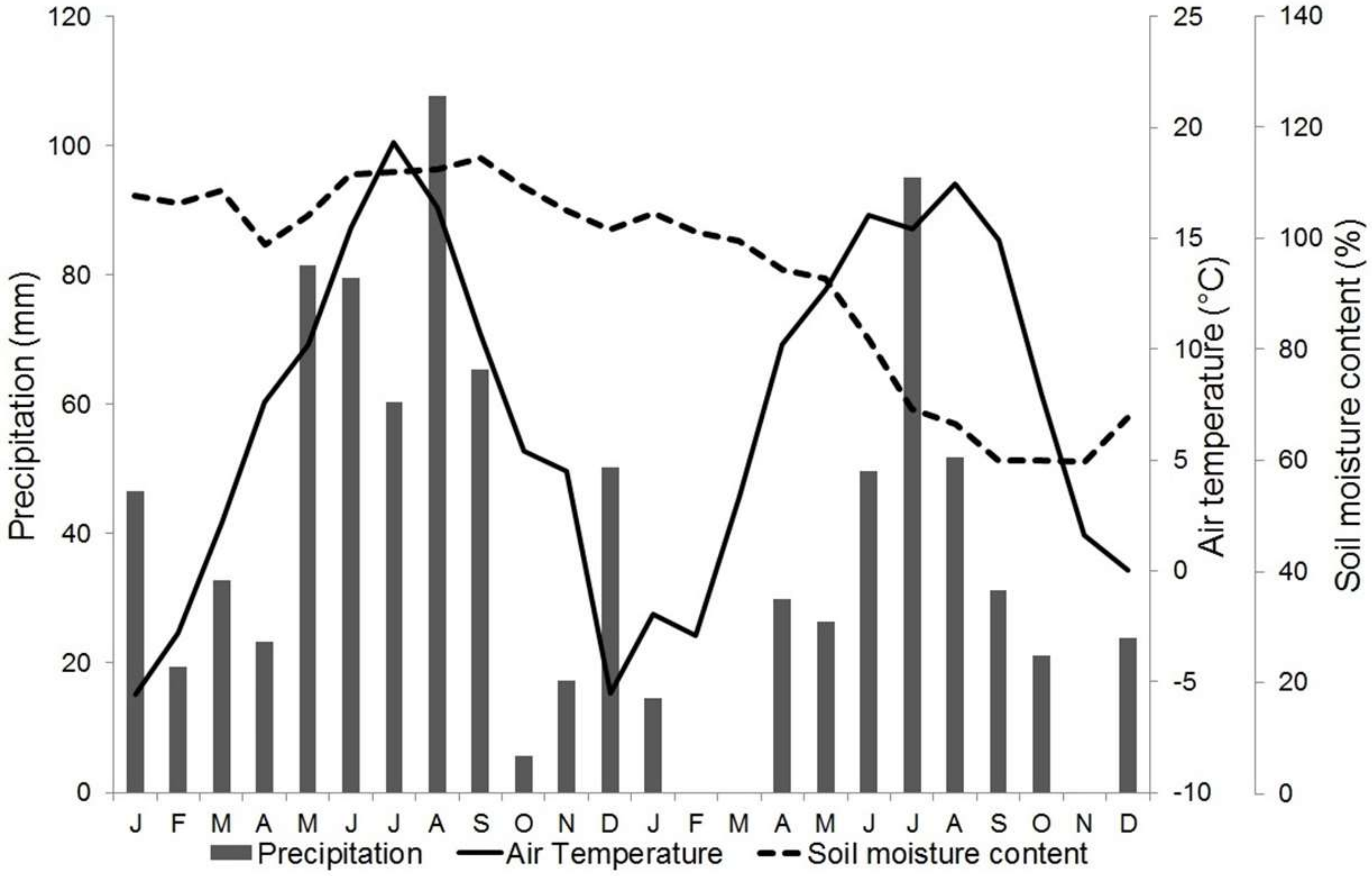
Long-term (1961–2011; Protivanov weather station) and examined years (2010–2011; Rajec-Domanka research plot) monthly weather conditions.

Month	J	F	M	A	M	J	J	A	S	O	N	D
Long-term temperature (1961–2011)	-4.27	-3.95	0.77	5.9	11.5	13.34	**15.93**	15.46	12.24	7.36	0.74	-1.8
Temperature 2010	-5.60	-2.80	2.20	7.60	10.20	15.50	**19.30**	16.40	10.70	5.40	4.50	-5.50
Temperature 2011	-1.97	-2.91	3.38	10.19	12.72	16.05	15.4	**17.47**	14.9	7.93	1.63	0.02
Long-term Precipitation (1961–2011)	25.7	23.3	23.8	29.1	55.5	**90.3**	44.9	68.3	62.1	28.8	27.6	34.2
Precipitation 2010	46.6	19.3	32.8	23.3	81.6	79.6	60.3	**107.7**	65.4	5.6	17.2	50.2
Precipitation 2011	14.6	0.0	0.0	29.9	26.5	49.7	**95.2**	51.9	31.2	21.2	0.0	23.9

Study site weather conditions

Air temperature, soil moisture content (SMC) and average monthly precipitation recorded at the Rajec-Domanka research plot (2010–2011)



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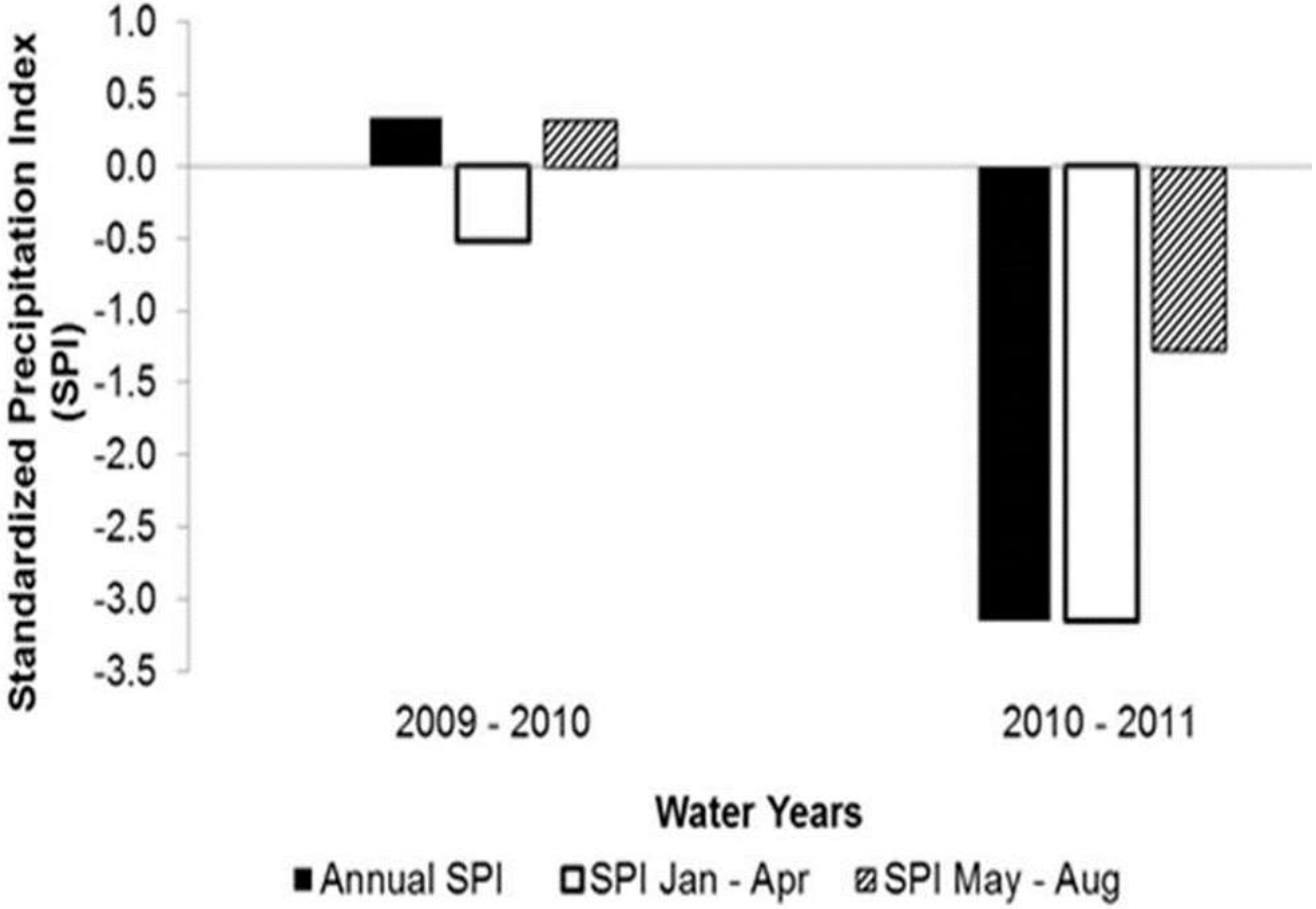
Study site weather conditions

Standardized Precipitation Index (SPI) depicting the severity of dry conditions during the examined years (2010–2011).

SPI values	Classification
2.0+	Extremely Wet
1.5 to 1.99	Very Wet
1.0 to 1.49	Moderately Wet
-.99 to .99	Near Normal
-1.0 to -1.49	Moderately Dry
-1.5 to -1.99	Severely Dry
-2 and less	Extremely Dry



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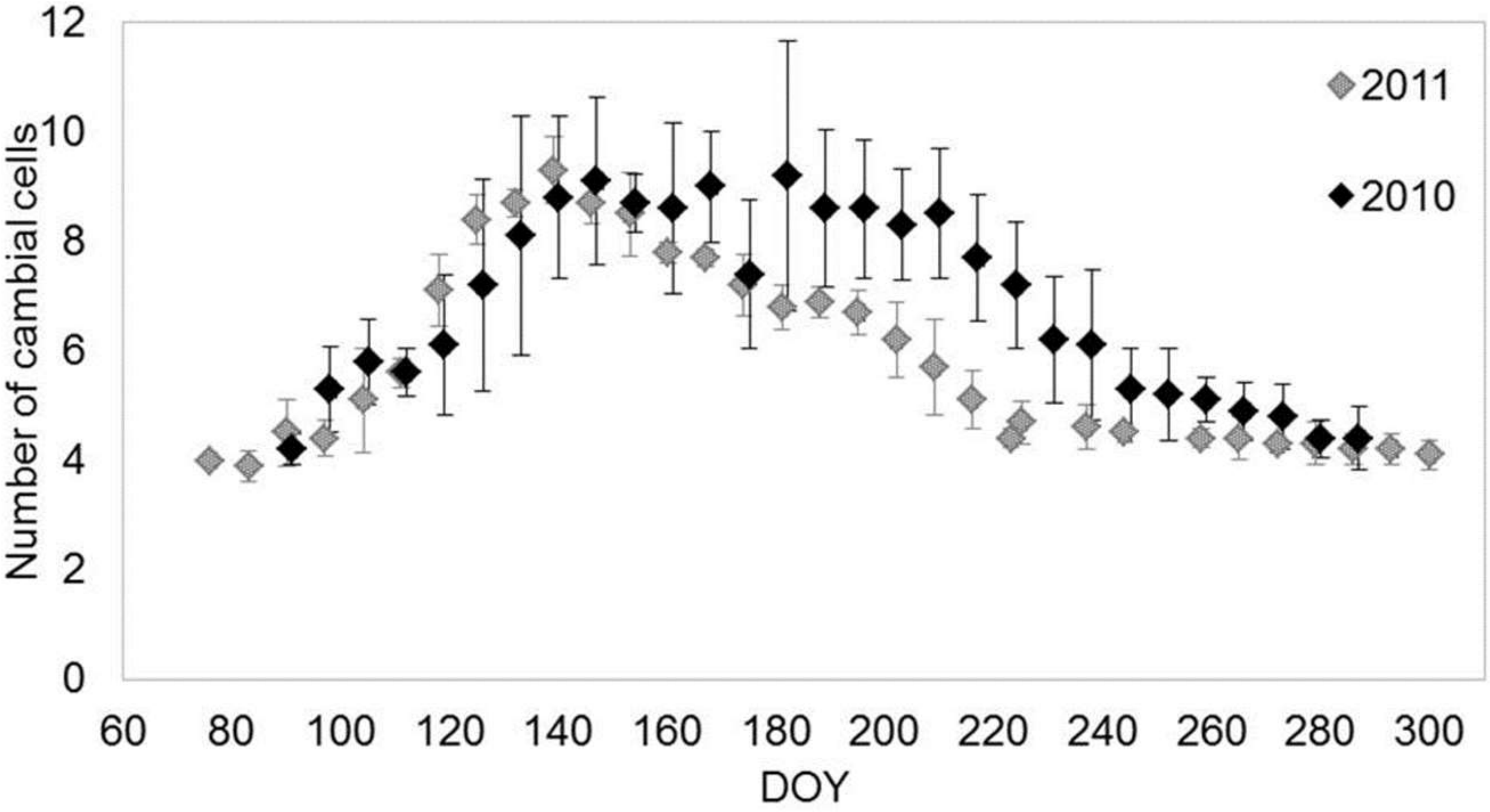
Findings of the research

Mean number of cambial cells during growing seasons 2010 and 2011. Standard deviation in error bars.



Wood phenological phases (onset, ending and duration) expressed in the Day of the Year (DOY) recorded for each tree.

Wood phenological phases	2010	2011	P - values
Onset of cambial cell production (DOY)	121 ± 6	112 ± 8	***
End of cambial cell production (DOY)	226 ± 6	206 ± 4	****
Onset of enlargement (DOY)	129 ± 4	126 ± 3	NS
End of enlargement (DOY)	235 ± 6	214 ± 4	****
Onset of secondary wall formation (DOY)	149 ± 4	136 ± 6	**
Onset of maturation process (DOY)	180 ± 3	174 ± 8	NS
End of maturation process (DOY)	266 ± 10	237 ± 6	***
Total duration of cambial cell production (in DOYs)	106 ± 11	93 ± 7	NS
Total duration of radial enlargement (in DOYs)	106 ± 9	88 ± 4	**
Total duration of maturation (in DOYs)	85 ± 10	63 ± 12	*
Total duration of growing period (in DOYs)	145 ± 10	125 ± 10	*

The DOYs represent mean values of the six trees per year (± symbol depicts the standard deviation). Significance (two sample t-test) presented in asterisks (*significant at $p < 0.05$, **significant at $p < 0.005$, ***significant at $p< 0.001$, **** significant at $p < 0.0001$, NS: not significant).

Findings of the research

Average air temperature and soil moisture content (SMC), 10 days before the onset and the ending of each wood phenological phase in 2010 and 2011.

Wood phenological phases	Air Temperature (^{o}C)			Soil Moisture Content (SMC %)		
	2010	2011	P - value	2010	2011	P -value
Onset of cambial cell production	9.6 ± 1.6	9.9 ± 4.0	NS	14.2 ± 1	12.7 ± 0.5	***
End of cambial cell production	17.7 ± 2.5	14.1 ± 2.1	*	12.2 ± 2	8.2 ± 2	***
Onset of radial enlargement	9.6 ± 1.6	7.8 ± 4.5	NS	17.9 ± 1	13.5 ± 0.4	****
End of radial enlargement	16.2 ± 3.0	13.3 ± 1.4	*	11.0 ± 1	7.3 ± 1	****
Onset of secondary wall formation	12.5 ± 1.1	13.5 ± 3.4	NS	18.4 ± 1	12.8 ± 2	***
Onset of maturation process	15.2 ± 1.9	16.5 ± 3.4	NS	13.2 ± 1	9.3 ± 1	****
End of maturation process	11.8 ± 1.5	20.8 ± 3.1	****	8.8 ± 1	5.8 ± 0.4	****
Total duration of cambial cell production	15.3 ± 5.9	14.6 ± 5.1	****	13.9 ± 4	10.8 ± 3	****
Total duration of radial enlargement	15.9 ± 5.8	15.2 ± 4.5	****	13.3 ± 4	10.0 ± 3	****
Total duration of maturation	16.2 ± 5.5	16.2 ± 4.5	NS	10.3 ± 2	7.2 ± 1	****
Total duration of growing period	14.70 ± 5.6	15.2 ± 5.0	***	13.0 ± 4	9.8 ± 3	****

Significance (two sample t-test) is presented with asterisks (* for $p<0.05$, ** for $p<0.005$, *** for $p<0.001$, **** for $p<0.0001$, NS: not significant).

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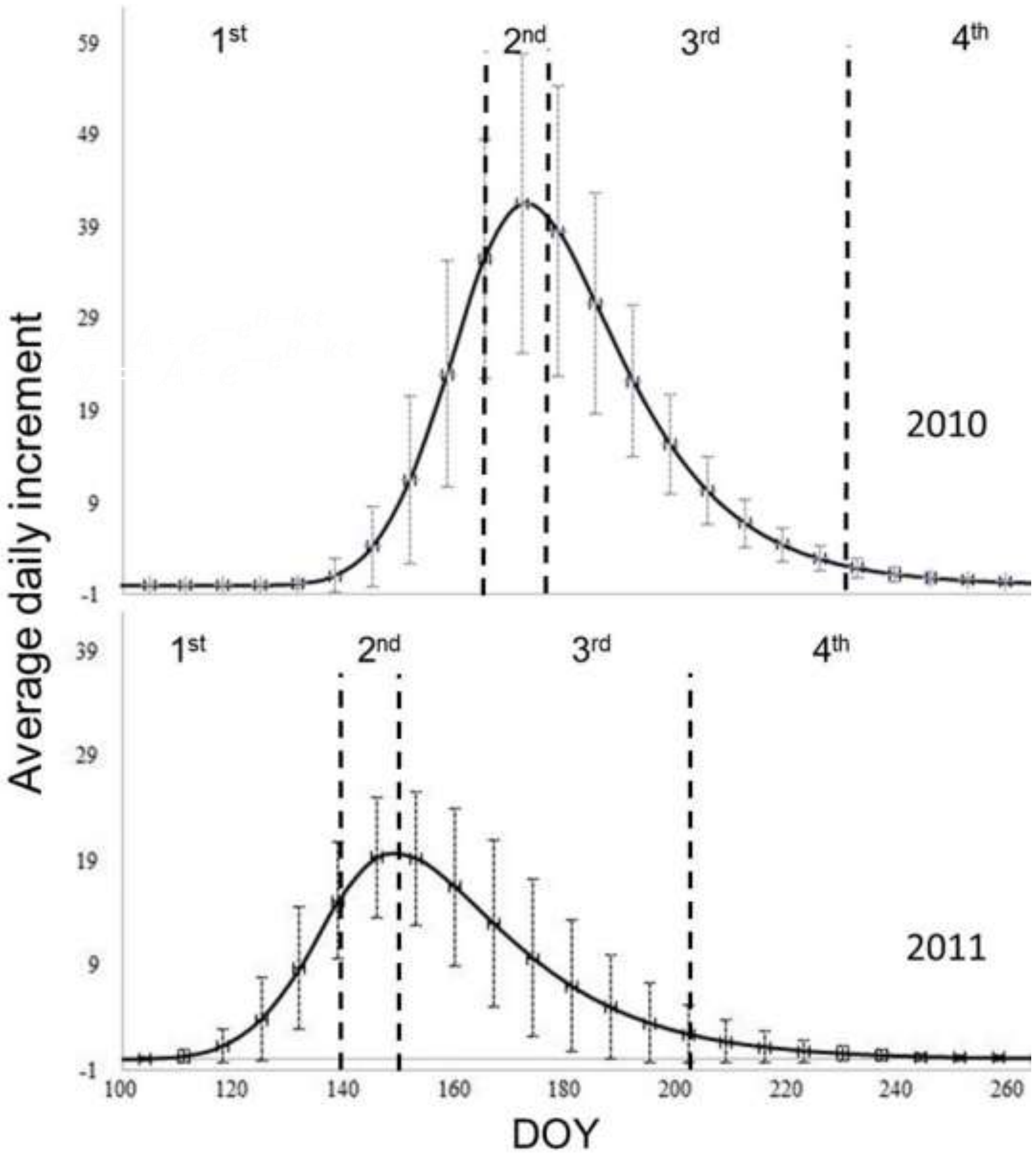
Findings of the research

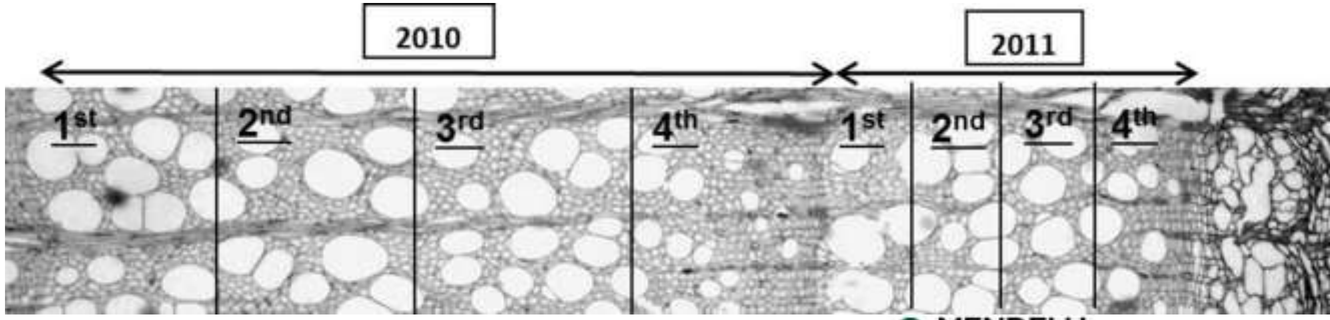


Average daily increment in 2010 and 2011 growing seasons, first derivatives of Gompertz function. Error bars show standard deviation.

$$y = A \cdot e^{-e^{B-k \cdot t}}$$

y is the weekly cumulative cells,
t is the day of year,
A is the upper asymptote, representing the maximum number of cells,
B is the place on the *x*-axis, estimating the beginning of cambial activity, and
k is the inflection point on the curve.

According to the first derivatives of the Gompertz function, each quarter was matched with the duration (in DOYs) needed to form the vessels



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Number of vessels (mm^{-2}), vessel diameter (μm) and percentage water conductive area (%) per quarter and year (one-way repeated measures ANOVA, $p<0.5$).

Quarter	Year	2010	2011	F	p
1st	DOY	126–164	104–138		
	No of vessels (mm^{-2})	**117±51**	**136±24**	**6.78**	**0.03**
	Vessel diameter (μm)	60±10	66±10	1.03	0.34
	Water conductive area (%)	43.3±32.2	49.0±18.7	1.74	0.21
2nd	DOY	164–176	138–149		
	No of vessels (mm^{-2})	**101±26**	**120±21**	**10.01**	**0.01**
	Vessel diameter (μm)	61±9	64±6	0.03	0.87
	Water conductive area (%)	41.6±25.2	42.7±16.9	3.24	0.105
3rd	DOY	176–191	149–161		
	No of vessels (mm^{-2})	86±33	132±34	2.2	0.17
	Vessel diameter (μm)	62±8	56±8	1.4	0.27
	Water conductive area (%)	33.8±21.3	39.2±18.2	2.49	0.149
4th	DOY	191–244	161–208		
	No of vessels (mm^{-2})	83±35	109±39	3.34	0.1
	Vessel diameter (μm)	**48±4**	**43±4**	**6.56**	**0.03**
	Water conductive area (%)	19.4±10.6	19.7±10.0	4.22	0.069

$$Water\ conductive\ area = \frac{\text{Total vessel area}}{\text{Tree ring area}} \times 100\ (\%)$$

Number of vessels (mm^{-2}), vessel diameter (µm) and percentage water conductive area (%) per quarter and year (one-way repeated measures ANOVA, p<0.5).

Quarter	Year	2010	2011	F	p
Average for the whole ring	No of vessels (mm^{-2})	97±16	124±12	7.5	0.033
	Vessel diameter (µm)	58±6.6	57±10.5	0.004	0.95
	Water conductive area (%)	34.5±10.9	37.6±12.6	1.135	0.72
	Tree ring width (mm)	**1392±677**	**847±178**	**18.32**	**0.002**
Average 1st-2nd	**No of vessels (mm^{-2})**	**109±39**	**128±23**	**13.36**	**0.0015**
	Vessel diameter (µm)	60±9	65±8	1.59	0.22
	Water conductive area (%)	**42.5±27**	**45.8±17.3**	**5.12**	**0.034**
Average 3rd-4th	**No of vessels (mm^{-2})**	**85±32**	**120±37**	**5.92**	**0.024**
	Vessel diameter (µm)	55±10	49±9	1.84	0.189
	Water conductive area (%)	**26.7±17.7**	**29.4±17.3**	**4.7**	**0.042**

Vessel diameter correlated (Pearson's correlation) with the weather conditions (temperature and soil moisture content - SMC).

	Vessel diameter							
Year	2010				2011			
Quarter	1st	2nd	3rd	4th	1st	2nd	3rd	4th
Period (in DOYs)	116–164	154–176	166–191	181–244	94–138	128–149	193–161	151–208
Mean Air Temp	**-.832***	.271	-.319	.040	.229	-.302	.096	-.515
Max Air Temp	-.510	.131	-.641	-.012	.577	-.904	.591	-.008
Min Air Temp	**-.794***	.025	.368	.243	.053	-.622	.104	-.470
Mean SMC	-.131	-.103	-.679	-.223	**.909***	.000	.537	**.862***
Max SMC	-.209	-.141	-.707	-.281	**.831***	-.687	.510	**.861***
Min SMC	.228	-.178	-.637	-.050	**.827***	.653	.498	**.867***

*. Correlation is significant at the 0.05 level (2-tailed).

No of vessels (mm^{-2}) correlated (Pearson's correlation) with the weather conditions (temperature and soil moisture content - SMC).

	No of vessels (mm^{-2})							
	2010				2011			
Quarter	1st	2nd	3rd	4th	1st	2nd	3rd	4th
Period (in DOYs)	116–164	154–176	166–191	181–244	94–138	128–149	193–161	151–208
Mean Air Temp	.060	.086	.111	-.446	.015	-.433	-.406	-.208
Max Air Temp	-.012	-.070	.652	-.479	-.034	-.302	-.094	-.049
Min Air Temp	.577	.049	-.408	-.396	-.179	-.383	-.503	-.242
Mean SMC	**.643**	-.238	**.831**	.128	.193	-.076	**.765**	**.693**
Max SMC	**.635**	-.168	**.850**	.185	**.667**	-.391	**.740**	**.697**
Min SMC	**.808**	-.198	**.797**	-.053	**.695**	.107	**.753**	**.638**

*. Correlation is significant at the 0.05 level (2-tailed).

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Percentage of water conductive area (%) correlated (Pearson's correlation) with the weather conditions (temperature and soil moisture content - SMC).

	Water conductive area (%)							
	2010				2011			
Quarter	1st	2nd	3rd	4th	1st	2nd	3rd	4th
Period (in DOYs)	116–164	154–176	166–191	181–244	94–138	128–149	193–161	151–208
Mean Air Temp	-.352	.114	.588	-.027	.095	.095	-.561	-.705
Max Air Temp	-.067	.045	.625	-.221	.215	.215	-.048	-.290
Min Air Temp	-.244	-.090	.351	.142	-.142	-.142	-.393	-.639
Mean SMC	.144	-.151	**.703**	.484	.593	.593	**.800**	**.769**
Max SMC	.112	-.098	**.692**	.515	**.918****	**.918****	**.762**	**.756**
Min SMC	.251	-.126	**.762**	.445	**.930****	**.930****	**.802**	**.791**

*. Correlation is significant at the 0.05 level (2-tailed).

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Conclusions

- Tree-ring formation patterns and vessel features showed different responses to climatic factors in the two years.
- In 2010, the onset of cambial cell production occurred almost 10 days later than in 2011.
- Lack of precipitation in 2011 caused premature cessation of cambial cell division and markedly narrower annual xylem increments.
- Vessel density and water conductive area were higher in 2011 than in 2010.
  Average vessel size did not change.
- In response to local weather conditions, beech controls its hydraulic conductivity mainly by changing the number of vessels and tree growth rate, followed by vessel size.

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Project Indicators of Trees Vitality Reg. No. CZ.1.07/2.3.00/20.0265

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Recent Publications

Fajstavr M*, Giagli K, Vavrčík H, Gryc V, Horáček P, Urban J (2020). **The cambial response of Scots pine trees to girdling and water stress**. IAWA 41: 159 – 185. DOI: https://doi.org/10.1163/22941932-bja10004

Fajstavr M*, Paschová Z, Giagli K, Vavrčík H, Gryc V, Urban J (2018). **Auxin (IAA) and soluble carbohydrate seasonal dynamics monitored during xylogenesis and phloemogenesis in Scots pine**. iForest 11: 553 – 562. DOI: 10.3832/ifor2734-011

Martinez del Castillo E*, Prislan P, Gričar J, Gryc V, Merela M, Giagli K, de Luis M, Vavrčík H, Čufar K (2018). **Challenges for growth of beech and co-occurring conifers in a changing climate context**. Dendrochronologia 52: 1 – 10 DOI: org/10.1016/j.dendro.2018.09.001

Fajstavr M*, Giagli K, Vavrčík H, Gryc V, Urban J (2017). **The effect of stem girdling on xylem and phloem formation in Scots pine**. Silva Fennica 51 (4): 22 (article ID 1760). DOI: org/10.14214/sf.1760

Giagli K*, Gričar J, Vavrčík H, Gryc V (2016). **Nine-year monitoring of cambial seasonality and cell production in Norway spruce.** iForest - Biogeosciences and Forestry 9: 375 – 382.

Kolář T*, Giagli K, Trnka M, Bednářová E, Vavrčík H, Rybníček M (2016). **Response of the leaf phenology and tree-ring width of European beech to climate variability.** Silva Fennica 50(2): 18 (article ID 1520). DOI: org/10.14214/sf.1520

Thank you for your attention

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