Long-term changes and drivers of leaf morphological traits of European beech and Norway spruce in Switzerland

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Motivation and Aims

Leaf morphological traits (LMT) of tree species have been observed to vary spatially across forest sites. However, longer-term records of LMT are often not easily available due to the missing measurements or systematic leaf archives. We thus lack an understanding on the long-term changes and drivers of LMT.

Here we make use of long-term LMT measurements and foliar material collections of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) trees from 1995 to 2019, which were performed within the Swiss Long-term Forest Ecosystem Research Program (LWF) (Fig. 1 and Tab. 1). Collection and measurements of foliar material, following the ICP Forests protocol, are conducted generally every second year.

Our main aims were

Determine long-term changes in LMT (i.e., leaf or needle mass, leaf area or needle length and the respective ratios of leaf mass per area or needle mass per length)

Identify the main drivers of LMT changes in time (e.g., climate (year of collection and previous year), macro-nutrients, fruiting intensity, crown transparency)

		Tab. 1 \rightarrow	Site name	Code Tree specie	Region	Latitude (N)	Longitud (E)	e Elevation (m a.s.l.)	MAT (°C)	MAP (mm)	DM100 (g)	LA or NL (mm ² or mm)	LMA or NML (gm ⁻² or mgcm ⁻¹)
Fagus sylvatica	Neunkirch	Site characteristics and average long-term LMT for the 11 stands of European beech and Norway spruce. Mean appual temperature (MAT) and mean appual	Alpthal	ALP Picea abies	Prealps	47°03'	08°43'	1160	6.4	2142	0.45 sd 0.11	11.87 sd 1.46	3.74 sd 0.639
Picea abies	Lägeren	precipitation (MAP) were calculated based on the LMT collection period of 1994-2019	Beatenberg	BEA Picea abies	Prealps	46°43'	07°46'	1510	5.2	1440	0.51 sd 0.13	11.69 sd 1.69	4.32 sd 0.679
	Othmarsingen (1)	DM100: dry mass of 100 leaves or needles LA or NL: leaf area (beech) or needle length (spruce)	Bettlachstock	BET Fagus sylvatica	Jura	47°14'	07°25'	1150	7.4	1494	11.39 sd 3.71	1429.73 sd 458.02	80.04 sd 10.99
	Plateau Schänis	LMA or NML: leaf mass per area (beech) or needle mass per length (spruce)	Chironico	CHI Picea abies	Southern Alps	46°27'	08°49'	1365	5.4	1587	0.45 sd 0.08	12.93 sd 1.97	3.46 sd 0.417
J-u ra	Alptal Alptal		Davos	DAV Picea abies	Alps	46°49'	09°51'	1650	3.2	1130	0.48 sd 0.10	11.95 sd 1.96	4.03 sd 0.544
	Pre - Alos Davos		lsone	ISO Fagus sylvatica	Southern Alps	46°08'	09°01'	1220	6.6	1792	14.10 sd 3.61	1585.29 sd 413.37	87.36 sd 9.13
	Beatenberg		Lägeren	LAE Fagus sylvatica	Central Plateau	47°28'	08°22'	680	9.1	1172	15.12 sd 3.31	1797.9 sd 284.22	84.44 sd 15.87
52 1	Chironico		"	" Picea abies	"	"	"	u	II	II	0.54 sd 0.11	15.31 sd 1.56	3.52 sd 0.609
-	and the support of the second		Lausanne	LAU Fagus sylvatica	Central Plateau	46°35'	06°40'	805	8.3	1233	11.30 sd 2.99	1533 sd 381.71	72.87 sd 14.38
S.	Isone Charles and Isone Charle		Neunkirch	NEU Fagus sylvatica	Jura	47°41'	08°32'	580	9.0	935	13.18 sd 3.69	1740.55 sd 499.21	77.25 sd 11.16
N	The second states	← Fig. 1	Othmarsingen	OTH Fagus sylvatica	Central Plateau	47°24'	08°14'	485	9.8	1049	14.13 sd 3.37	1793.15 sd 482.30	81.17 sd 11.15
A	Kiematana Y W	Locations of the 11 study sites distributed across Switzerland with the investigated main tree species	Schänis	SCH Fagus sylvatica	Central Plateau	47°10'	09°04'	710	8.1	1829	11.63 sd 2.77	1660.96 sd 314.84	69.78 sd 12.52
10 20 40	60 80 WSL/LWF, Flurin Sutter, 2021	European beech and Norway spruce	Ranges					485 - 1650	3.2 - 9.8	935 - 2142	11.30 - 15.12 or 0.45 - 0.54	1429 - 1793 or 11.69 - 15.31	69.78 - 87.36 or 3.46 - 4.32

Results and Outcomes

1) We observed clear changes over the study period in LMT of beech and spruce, with strong year-specific effects (e.g., 2011) (Fig. 2 and Tab. 1 for ranges)



2) The linear mixed models' selection (**Tab. 2**) shows that the drivers of the changes of beech and spruce LMT largely differ from each other and are mostly a combination of different variables

Variable	Estimate	SE	$\mathbf{R}^2\mathbf{m}$	$\mathbf{R}^2 \mathbf{c}$	
seeds2	-391.817 ***	70.840			
seeds1	-204.295 **	59.648			
TotDef	-112.948 ***	25.211	0.70	0.73	
dpT_SON	110.924 ***	27.754	0.70	0.75	
elevation	-106.434 *	34.372			
N	82.382 **	29.199			
Beech - Ar Variable	ea Estimate	SE	R ² m	R ² c	
elevation	-2.341 **	0.455			
Ca	-2.264 ***	0.378			
Р	-1.623 ***	0.362	0.61	0.66	
Ν	1.360 ***	0.338			
dpT_SON	1.113 ***	0.241			
Beech - LN Variable	/IA _Estimate	SE	R ² m	R ² c	
Р	-5.687 ***	1.065			
seeds2	5.436 **	1.936		0.78	
Ca	-5.248 ***	1.323	0.65		
dpVPD_JJA	5.168 ***	0.839	0.03		
ceede1	3.995 *	1.657			
secusi			1	1	

Variable	Estimate	SE	$\mathbf{R}^2\mathbf{m}$	$\mathbf{R}^{2}\mathbf{c}$
dVPD_MAM	-0.071 ***	0.012		
dETAP_yr	-0.030 **	0.010	0.58	0.75
dP_SON	-0.030 **	0.010		
K	-0.026	0.018		
dP_JJA	0.014	0.012		
Mø	0.013	0.015		

Variable	Estimate	SE	$\mathbf{R}^2\mathbf{m}$	\mathbf{R}^2 c
dVPD MAM	-0.813 ***	0.149		
elevation	-0.621	0.473		
dP_MAM	-0.563 ***	0.136		
dT_SON	-0.370 **	0.114		0.84
Ca	-0.254	0.281	0.65	
TotDef	-0.228	0.251		
dpSWB_yr	-0.043	0.108		
dSWB_yr	-0.037	0.098		
Spruce - NMI	r			
Variable	Estimate	SE	R ² m	R ² c
Variable P	Estimate 0.244 ***	SE 0.059	R ² m	R ² c
Variable P K	Estimate 0.244 *** -0.162	SE 0.059 0.122	R ² m	R ² c
Variable P K dpVPD_MAM	Estimate 0.244 *** -0.162 0.071	SE 0.059 0.122 0.059	R²m 0.41	R²c
Variable P K dpVPD_MAM dP_JJA	Estimate 0.244 *** -0.162 0.071 0.039	SE 0.059 0.122 0.059 0.056	R²m 0.41	R²c 0.83

← Tab. 2

Best models selection for each LMT and tree species. Each numeric variable has been scaled to ensure the comparability of the estimates. Marginal R^2 (R^2m) and conditional R^2 (R^2c) have been calculated based only on the best models and not the averaged models (relevant only for spruce in this case)

← Variables' description

Climate variables and drought indexes: Prefixes: "d" indicates deviation from long-term mean; "p" indicates previous year Suffix: "yr" indicates yearly value (relevant for drought indexes SWB and ETAP) T: temperature; P: precipitation; VPD: vapor pressure deficit; SWB: site water balance; ETAP: ratio between actual (ETa) and potential (ETp) evapotranspiration Meteorological seasons: DJF, MAM, JJA, SON Foliar nutrient and carbon concentrations: Ca, Mg, K, P, S, C, N

Trees' characteristics: TotDef: Total crown defoliation Seeds0: no fruits/seeds Seeds1: some fruits/seeds Seeds2: many fruits/seeds

Fig. 2

Mean LMT over time per plot and overall. In 2001 no beech samples were available to measure and in 2016 only samples from SCH were exceptionally measured.

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Materials and Methods

1) We completed and corrected the LMT measurements using archived foliar samples

2) We performed exploratory spatial analysis of the LMT by univariate linear regression (not shown)

We fitted and selected linear mixed models to investigate long-term drivers of LMT changes







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