Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland)

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Abstract

The effects of drought on radial growth of *Pinus sylvestris* were investigated by comparing sites along hydric gradients. The gradients were located in Valais, an inner Alpine dry valley in Switzerland, with each consisting of two site types, an extreme dry, xeric site and a less dry, moderate site. The two site types were assigned to phytosociological associations within the Erico-Pinion. The investigation covered the responses of tree growth to climate and particularly concentrated on intra-annual features of tree-rings such as earlywood/latewood ratio, intra-annual density fluctuation (IADFs) and traumatic tissues (TTs) as well as the sapwood/heartwood ratio. Radial growth differed according to the site types, with trees on dry sites generally showing more missing rings, lower mean ring widths, lower autocorrelation, higher mean sensitivities, reduced latewood proportions and lower sapwood areas than trees on moderate sites. The relationships between climate and tree-ring width, studied using response function analysis, varied strongly between the site types within the Erico-Pinion: Tree growth on dry sites was positively influence by precipitation at the end of the winter and the beginning of the growing season and negatively influence by temperature in June. Winter precipitation was positively correlated with radial growth, demonstrating its importance for the successful root and shoot growth of the plants in spring on dry sites. On moderate sites, tree growth was less controlled by climate than by prior growth. The intra-annual density fluctuation (IADFs) provided a valuable means to differentiate between the site types. In comparison to the moderate sites, the trees on dry sites contained more IADFs, and their frequency was increased. Moist-cool conditions in the middle of the growing season were the triggering factor for IADFs on dry sites, whereas on moderate sites, there must be an additional warm period in early summer in order to initiate IADFs. Most IADFs were found in latewood. We found no relationship between climate and traumatic tissues (TTs). It is unclear whether other abiotic or biotic factors such as wounding by insects or birds are responsible for the development of TTs. The assignment of these differences in tree growth behaviour to phytosociological associations will enable a deeper understanding of the site types and will facilitate the comparison with similar studies. Furthermore, the results can be combined with studies from other scientifi disciplines concerning these phytosociological associations. The ecological indicator values of the vegetation was a precise method for the distinction of site types.

Introduction

Tree-rings are integrative parameters of tree growth-influencin factors at a specifi site (Fritts 1976; Schweingruber 1996). The problem facing tree-ring analysis is to extract the signal of interest and to distinguish this signal from the background noise. Extreme sites, such as the upper tree-line or dry sites, have been the most valuable for dendroclimatological and dendroecological purposes, as the number of important influencin factors is reduced and the possibili-

ties for the interpretation of growth patterns are increased.

Tree growth on dry sites is highly dependent on precipitation. Numerous dendroclimatological investigations have been conducted for the semi-arid zones of North America (e.g. Glock (1955); Fritts (1974); Meko et al. (1980); Michaelsen et al. (1987); Blasing et al. (1988); Orwig and Abrams (1997)), and precipitation regimes have been reconstructed (D'Arrigo and Jacoby 1991; Grissino-Mayer 1996; Hughes and Graumlich 1996). In Europe, tree growth–precipitation relationships have been investigated for several regions, including southern France (Tessier 1982), Switzerland and Cyprus (Kienast et al. 1987), southern Spain (Gutierrez 1989), northern Germany (Riek et al. 1995; Krause and Eckstein 1993), and Austria (Oberhuber et al. 1998). All these dendroclimatological studies are based on *Pinus sylvestris*. The ecological interpretations of these studies are difficult as the sites were chosen using biogeographical criteria, such as climate type, vegetation level, types of bedrock or soil types. Ecological investigations involve more precise characterisation of the study sites. Although phytosociological units have the advantage of integrating the site characteristics of forest stands and are therefore suitable for describing the ecological situation of a sampling area, very few dendroecological investigations have been based on them (Lingg 1986; Rolland et al. 1999).

Dendroclimatological and dendroecological investigations mostly concentrate on tree-ring width or maximum latewood density for revealing general interactions between climate, tree growth and site conditions. Tessier et al. (1997) have suggested incorporating intra-annual features or anomalies in radial growth, as these can be useful tools for ecological and climatological interpretation, as demonstrated by Sellin (1994); De Kort (1993) for the earlywood/latewood ratio, Cherubini et al. (1996); Lepage and Bégin (1996) for compression wood, Swetnam (1993); Cherubini et al. (1996) for scars,Reid and Watson (1966); Wimmer and Grabner (1997) for traumatic resin ducts and pitch pockets, Czokajlo et al. (1997); Rigling and Cherubini (1999) for missing rings, Glerum and Farrar (1966); LaMarche and Hirschboeck (1984) for frost rings, and Filion et al. (1986) for light rings. In this context, intra-annual density fuctuations (IADFs), also known as false rings, double rings or multiple rings, could be a suitable proxy for estimating climate variability within a growing season (e.g. Wimmer and Strumia (1998)). IADFs are anomalies in ring growth that are formed by latewood-like cells within the earlywood or earlywood-like cells within the latewood (Fritts 1976). According to Schweingruber (1980), processes of cell wall enlargement and cell wall thickening are involved in the development of IADFs.

The aim of this study was to reveal the effect of drought on radial growth of *Pinus sylvestris* by analysing intra-annual features of tree-rings such as earlywood/latewood ratio, IADFs and traumatic tissues (TTs), as well as the sapwood/heartwood ratio. The value of phytosociological associations for describing site conditions and for distinguishing dry sites was tested, and the variation of the relationship between climate and tree growth on the dry sites of the Erico-Pinion was analysed.

Material and methods

Site descriptions

The six study plots are located in Valais, an inner Alpine dry valley in Switzerland (Figure 1), near the villages Varen (VA), Leuk (LE), and Getwing (SG). The study plots were grouped in three pairs, each consisting of a site subject to drought stress (VA-d, LE-d, SG-d) and a nearby moderate, less stressed site (VA-m, LE-m, SG-m). The dry-site stands were located on steep, south-facing slopes with high insolation, whereas the moderate site type stands were situated in less extreme conditions (Table 1). The site types also differed in their soil conditions: The dry stands grew on shallow soils on solid rock – Rendzic and Lithic Leptosols according to the FAO classifcation system (Soil map of the world, revised legend 1988) – with generally low water-holding capacities. The moderate stands grew on deep Calcaric Regosols (Soil map of the world, revised legend 1988) on loose moraine material with higher water-holding capacities. Determination of the rooting depth in soils on solid rock is impossible because roots grow into crevices. It was therefore impossible to calculate the water-holding capacity of the whole rooting zone of the soils. We calculated the water-holding capacity of the upper layers (0–30 cm soil depth) using estimates of the sand, silt, clay and stone and organic matter contents (Benzler et al. 1982).

The basis for the nomenclature of taxa and syntaxa was Aeschimann and Heitz (1996). Phytosociological relevées, following the methods of Braun-Blanquet
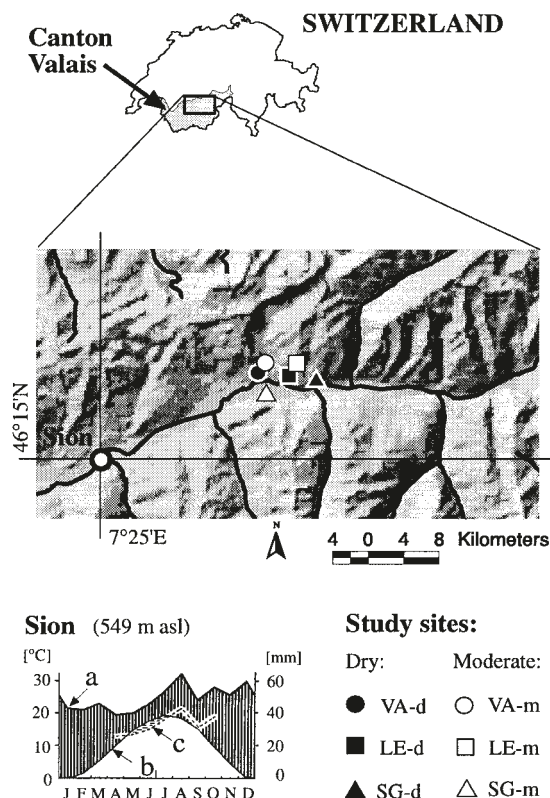
Figure 1. Geographic position of the study site in Valais and the climatic diagram for the meteorological station Sion, Switzerland (Walter and Lieth (1960), modif ed). The diagram consists of the monthly mean of precipitation ('a') and temperature ('b'), and the time span of water def cit ('c') (dotted line under line 'b').

(1964), were carried out and processed to identify differentiating species and ecological indicator values (Landolt 1977). According to Braun-Blanquet (1961); Plumettaz Clot (1988), the forests on the dry sites were assigned to the Odontito-Pinetum sylvestris association and the moderate sites to the Ononido-Pinetum sylvestris association.

Climatic data

The mean annual temperature of the study area is 9.7 °C (Figure 1). According to Walter and Lieth (1960), ten months per year have mean monthly temperatures above 0 °C. The mean annual precipitation is 590 mm. Precipitation is almost evenly distributed over the year, with a slight maximum in summer. Winter precipitation is of great importance for the yearly water regime. The relationship between precipitation and temperature during summer (Figure 1, arrow c) indicates a period of water def cit. The climatic

data that we used consisted of monthly values for precipitation (sum) and temperature (mean) from the nearby meteorological station at Sion.

Sampling and standard dendrochronological methods

At each site, diameter at breast height (DBH) and tree height were measured within an area of 20 by 20 m for each tree taller than 1.3 m, and stem basal area was calculated. For dendrochronological purposes, 12 trees (dominant or codominant) per site were sampled, taking two increment cores from each tree at breast height (1.3 m). The core sampling excluded reaction wood. Sample processing followed Pilcher (1990). If we did not reach the pith, the missing years were estimated according to the method of Bräker (1981). In measuring tree-ring width, we distinguished between earlywood width and latewood width. The measurements were made using the linear table Lintab (Rinn S.A., Heidelberg, Germany) and the Time Series Analysis and Presentation program TSAP (Rinn 1996).

All cores were synchronised by crossdating, a procedure for matching variations in ring widths among several tree-ring series. This enables the identif cation of the exact calendar year in which each tree-ring was formed (Fritts 1976). We used the procedure implemented in the TSAP-program (Gleichläuf gkeit values and Student's t-test) and combined the single curves into tree mean-curves and site chronologies.

The low-frequency variability in individual tree-ring series attributable to tree ageing, foreststand development or differences in the vitality of individual trees was removed by standardising the data using the Hugershoff equation (Warren 1980; Bräker 1981, 1996). This function is a combined polynomial and negative exponential and has only one turning point with increasing age.

The visual distinction between sapwood and heartwood was based on the change of the wood colour from yellowish to reddish-brown.

Correlation analysis and response functions

Dendroclimatic analyses were undertaken using response functions (Fritts et al. 1971; Serre-Bachet and Tessier 1990). The PRECON-program (Fritts and Shashkin 1995), applying the bootstrap method (Guiot 1991) with 50 replication steps, was adopted for the analyses. Response functions were calculated us-

Table 1. Site information

	VA-d	VA-m	LE-d	LE-m	SG-d	SG-m
Site name	Varen dry	Varen moderate	Leuk dry	Leuk moderate	Getwing dry	Getwing moderate
Coordinates	46°24'N 7°40'E	46°24'N 7°40'E	46°24'N 7°48'E	46°24'N 7°48'E	46°22'N 7°69'E	46°18'N 7°41'E
Altitude [m a.s.l.]	1060	1110	1000	1020	700	540
Exposition	South	South-east	South	South-east	South	–
Slope [%]	100	10 to 25	90	5 to 25	70	0
Vegetation type	Odontito-Pinetum	Ononido-Pinetum	Odontito-Pinetum	Ononido-Pinetum	Odontito-Pinetum	Ononido-Pinetum
Main tree species	Scots pine	Scots pine; Norway spruce	Scots pine	Scots pine	Scots pine	Scots pine
Stand structure	two-storeyed gapped	two-storeyed closed	two-storeyed gapped	three-storeyed closed	two-storeyed gapped	single storied closed
Tree cover [%]	65	90	60	85	55	75
Mean tree height [m]	7.5	19.8	5.5	16.1	5.5	17.3
Basal area [m²/ha]	34.5	74.1	35.5	53.6	16.5	60
Soil substrate	Solid rock Limestone	Moraine Limestone	Solid rock Limestone	Moraine Limestone	Solid rock Limestone	Moraine Limestone
Soil type (FAO)	Rendzic Leptosol	Calcaric Regosol	Lithic Leptosol	Calcaric Regosol	Rendzic Leptosol	Calcaric Regosol
Waterholding capacity (soil depth 0–30 cm [mm])	32	70	45	66	29	72

ing the detrended master chronologies for each site and the mean monthly temperature and precipitation sums from June to December of the previous year and from January to October of the current year. The response functions were calculated with three years' prior growth. The coefficients were calculated for a uniform 95-year period (1901–1995), and the significantly influencing months were determined at the 90%, 95% and 99% confidence levels.

Intra-annual features

The intra-annual features, such as IADFs and TTs, were examined with the aid of a stereo binocular using magnifications up to 20-fold (Figure 5). They were dated and assigned to earlywood or latewood subjectively. In some cases, IADFs were identified only through cross-dating.

The relative proportion and frequency of intra-annual features was calculated. The changing sample depth over time generates a bias for the frequency variance. The scaling suggested by Osborn et al. (1999) was applied to improve the stability of variance:

$$N_{stab} = \left(\frac{n_x}{N}\right) N^{0.5}$$

F_{stab} = Frequency stabilized
n_x = Number of IADFs or TTs
N = Number of observed tree-rings

Results

The mean ecological indicator values (Landolt 1977) showed a clear differentiation between the two site types. The values indicated that the dry sites had more alkaline soils with higher permeability and less humus in the upper soil layer than the moderate sites. In addition, the dry sites were sunnier and more exposed to high temperatures than the moderate sites. The indicator values for nutrients (not shown in the graph) were around 2 for both, the moderate and the dry sites, indicating poor soils. The indicator values for continentality (not shown in the graph) distinguished between the site types, with values from 3.0 to 3.4 for the moderate sites meaning tempered and balanced climate, and with values between 3.6 and 3.7

for the dry sites indicating relatively continental climate.

The mean tree height plotted against basal area (Figure 2d) showed a clear differentiation between the site types, with basal areas of less than 35 m²/ha and mean tree heights of less than 7.5 m for the dry sites, and higher basal areas (> 50 m²/ha) and mean tree heights (> 16 m) for the moderate sites. The heights of single trees, but not the DBHs, could be used for the distinction of the site types (Figure 2e).

Tree-ring chronologies

The mean tree-ring width chronologies for the six study sites illustrate the different growth behaviours of the stands (Figure 3). Diameter growth at the moderate sites is in general higher than growth at the dry sites. The growth characteristics of the dry stands differ from the others, as shown by the descriptive statistics in Table 2.
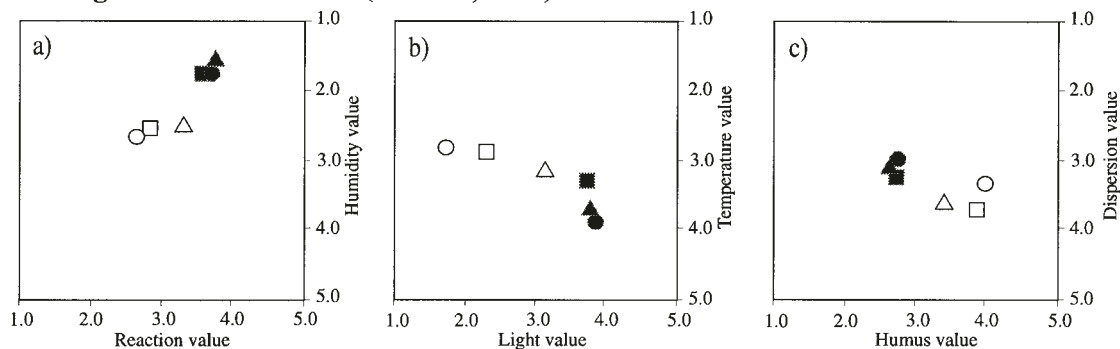
The lengths of the chronologies within the site pairs VA and LE are similar, with differences of less than 40 years between the older moderate and the younger dry stands. In the SG site pair the chronology of the dry stand is 60 years longer than that of the moderate stand. The trees on dry sites generally show more missing rings and have lower mean and median values for tree-ring widths than on moderate sites. The range of mean ring widths for all stands varies from 0.80 to 1.17 mm and is similar to the dry *Pinus sylvestris* forests investigated by Kienast et al. (1987) from Valais and Jura in Switzerland (0.46–1.28 mm) and by Oberhuber et al. (1998) for the Inn valley in Austria (0.54–0.89 mm). Tessier (1982) found higher values (0.83–1.49 mm) for the French Alps.

The first order autocorrelation, a measure of the influence of the previous year's growth on growth in the current year (Fritts 1976), is relatively high for all sites. The comparison by site pairs shows higher values for the moderate sites (0.69-0.80) than for the dry sites (0.42–0.75). Sensitivity is a measure of the mean relative changes between adjacent ring widths (Fritts 1976). The variation of mean sensitivity for the dry stands (0.18–0.25) was similar to the above studies (0.13–0.23). The moderate stands were relatively complacent (0.15–0.17).
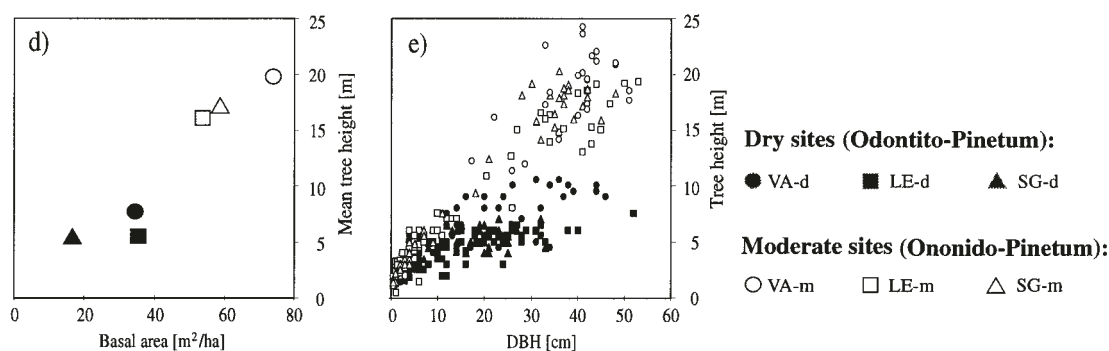
The distribution patterns of ring widths, described by skewness and kurtosis, show deviations from the standard normal distribution, with a value of 0 for both indicating that the distribution is symmetric and

Ecological indicator values (Landolt, 1977):

Growth parameters:

Figure 2. Ecological indicator values of the vegetation: a) Reaction value indicates the acidity of soils, from 1.0 (acid soils) to 5.0 (alkaline soils); humidity value indicates an average humidity of the soils, from 1.0 (very dry) to 5.0 (waterlogged). b) light value indicates the light intensity, from 1.0 (very shady) to 5.0 (full light); temperature value indicates the average temperature during growing season, from 1.0 (cool) to 5.0 (hot). c) humus value indicates the humus content of the upper soil, from 1.0 (mineral soil) to 5.0 (rich in humus); dispersion value indicates the particle size of the soils and the aeration, from 1.0 (cliffs and rocks) to 5.0 (clay soils). Growth parameters of stands d) and single trees e). DBH = diameter at breast height.

normally distributed (Sachs 1978). The trees on all sites except LE-m showed positive values for skewness and kurtosis, meaning that the distributions were oblique to the left and excessive. No difference existed between the site types.

The expressed population signal (EPS) indicates the degree to which the particular sample chronology portrays a hypothetically perfect chronology (Wigley et al. 1984). The EPS-values were higher for all stands (except VA-d latewood) than the critical level of 0.85 suggested by Wigley et al. (1984), meaning that the chronologies are representative of tree growth in the stands.

Latewood width showed similar results to ring width.

The relationship between earlywood width and latewood width was calculated for a f xed time span of 50 calendar years from 1946 to 1995 and for individual ring ages between 51 and 100 years. The trees

on dry sites showed signif cantly higher ratios than trees on moderate sites. Latewood width and ring width were positively correlated for both the dry and the moderate stands, corresponding with the results of De Kort et al. (1991).

On dry sites, trees had signif cantly lower sapwood areas, basal areas and less distinct heartwood areas than trees on moderate sites (Table 3). The number of sapwood rings did not change consistently between the site types.

Climate–growth relationships

The response functions in Figure 4 describe the relationships between tree-ring width, latewood width and climate (Fritts 1974). The general correlation patterns for both the dry and the moderate stands, for tree-ring width and for latewood width, were mostly
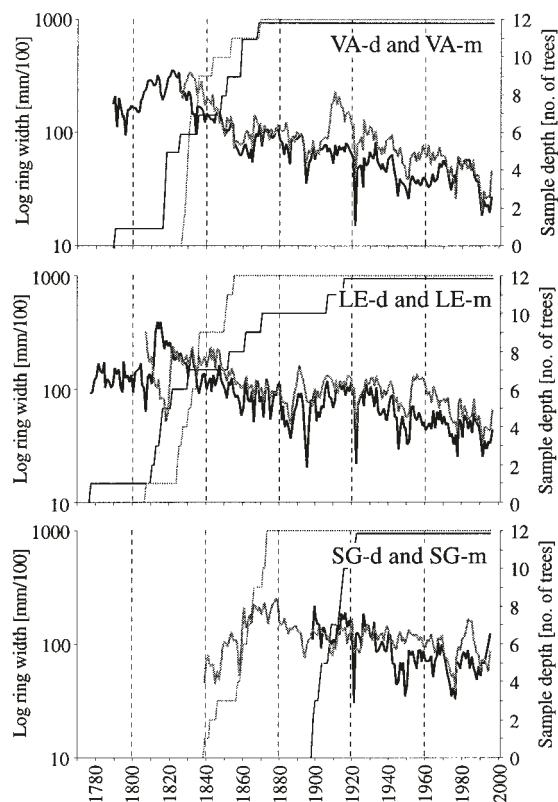
Figure 3. Tree-ring chronologies for the dry (black lines) and moderate sites (grey lines)

positive for precipitation and negative for temperature.

Tree-ring width at the dry stands was positively correlated with precipitation during the growing season in April and May, during winter in December, January (VA-d) and March and in previous year's August (LE-d) and September (SG-d). Temperature showed signif cant negative correlations with tree growth in April (SG-d), June, August (VA-d) and December (VA-d) of the previous year, but with only a few signif cant positive correlations. The moderate sites showed few signif cant signals, and no common pattern existed among the sites.

In comparison to the moderate stands, latewood width of rings from trees in the dry stands showed weaker signals for precipitation in April and December and lacked the signif cant positive correlation in May. In addition, signif cant positive correlations appeared in June, July and August. In contrast to ring width, the response of latewood to temperature showed negative correlations in April, June, August and October of the current year and September and December of the previous year.

The moderate stands, except for VA-m, in general showed weaker signals for precipitation than the dry stands, and the temperature response from April to June of the current year was also reduced. Consistent with the lower f rst order autocorrelation of tree growth on dry sites, the response of prior growth was also reduced.

The regression models of the response functions at the dry sites showed a higher proportion of the variance explained by climate for tree-ring width and more pronounced for latewood width than at the moderate sites. The latter had higher proportions of prior growth explaining the total variance.

The dependent verif cation regression coefficients of the response functions, using the bootstrap method of Guiot (1991), ranged from 0.867 ± 0.031 to 0.914 ± 0.023 for tree-ring widths and from 0.853 ± 0.030 to 0.910 ± 0.031 for latewood width. The independent verif cation regression coefficients ranged from 0.576 ± 0.100 to 0.725 ± 0.084 for tree-ring widths and from 0.484 ± 0.117 to 0.705 ± 0.087 for latewood width. The moderate stands had slightly lower values than the dry stands for both the dependent and the independent coefficients.

Intra-annual features

We also examined IADFs (intra-annual density f uctuations) and TTs (traumatic tissues) (Figure 5). The relative positions of these intra-annual features within a tree-ring varied from earlywood to latewood, depending on the time of occurrence of the triggering factor, on the individual situation of the tree (microclimate, f tness, etc.), and on the position on the tree where sampling took place. Frequently, more than one IADF was observed in a single tree-ring.

The descriptive statistics of the IADFs (Table 4) indicate a differentiation between the site types for various parameters. Every core of a tree grown on a dry site contained at least one IADF. However, on moderate sites only 67 to 92% of the cores showed IADFs. A total of 21,158 tree-rings were examined, varying in number between the sites from 2,330 to 3,912. The stabilized mean IADF frequency was higher for trees growing on dry sites (3.37 to 7.64) than on moderate sites (1.49 to 2.76). Most of the IADFs were located in latewood.

The descriptive statistics of the TTs (Table 4) show weaker differences between the site types. On site SG-m, 67% of the cores contained TTs, which is similar to the dry site SG-d, but the frequency of TTs was

Table 2. Descriptive statistics of the ring width and latewood width chronologies.

	VA-d	VA-m	LE-d	LE-m	SG-d	SG-m
Beginning	1789	1826	1776	1806	1898	1839
End	1995	1995	1995	1995	1995	1995
Nb. of years, maximum	206	169	219	189	97	156
Nb. of years, stand.dev.	23.5	12.4	40.7	13.3	8.1	11.7
Nb. of missing rings	8	0	18	2	3	0
Missing rings [%]	0.02	0	0.47	0.05	0.13	0
Tree-ring width						
Mean [1/100 mm]	82	103	80	97	91	117
Median [1/100 mm]	61	86	62	90	80	106
Mean sensitivity[1]	0.18	0.17	0.25	0.17	0.23	0.15
Standard deviation[1]	283.88	362.81	349.53	301.58	286.66	243.43
Skewness[1]	0.68	1.48	1.70	0.34	0.13	0.33
Kurtosis[1]	1.21	3.15	8.45	−0.39	0.40	0.77
First order autocorr.[1]	0.75	0.80	0.55	0.74	0.42	0.69
EPS[1][2]	0.85	0.95	0.90	0.93	0.92	0.89
Latewood width						
Mean [1/100 mm]	30	32	20	25	24	37
Median [1/100 mm]	23	29	17	24	21	38
Mean sensitivity[1]	0.28	0.27	0.39	0.27	0.41	0.23
Standard deviation[1]	390.98	464.27	427.81	419.12	379.50	320.65
Skewness[1]	0.84	1.51	0.97	1.32	0.54	0.30
Kurtosis[1]	1.88	3.83	1.28	3.33	0.38	0.21
First order autocorr.[1]	0.61	0.67	0.33	0.55	0.11	0.59
EPS[1][2]	0.82	0.95	0.87	0.91	0.92	0.88
Relation EW/LW[3]						
1946–1995	2.81	2.62	4.41	3.55	3.71	2.46
Ring age 51–100	2.65	2.14	3.87	3.08	3.62	1.88

[1] from standardised data series
[2] Expressed Population Signal
[3] Earlywood/latewood ratio

lower. The two sites VA-m and LE-m had very few TTs.

We investigated the relationships between the stabilized frequencies of IADFs and TTs, respectively, and ring width and ring age. We tested all the rings containing IADFs or TTs against the rings without IADFs or TTs using the Kolmogorov-Smirnov test (Sachs 1978). For all stands, tree-rings containing IADFs were signifcantly younger and wider than those without IADFs (p < 0.001). In the case of TTs, only the dry stands showed this relationship, whereas the moderate stand SG-m showed no correlation. The stands LE-m and VA-m could not be analysed because the TT frequency was too low.

The dry and moderate sites were combined to build master chronologies of stabilized frequencies of IADFs and TTs in order to achieve a more homogenous distribution of the signals over time (Figure 6). The distributions of IADFs and TTs in relation to calendar years varied between the site types. The trees on moderate sites contained fewer IADFs and only a few TTs. The frequency of IADFs was higher than 2 in 1789, 1825, 1873, and 1930 on the dry sites, but only in 1859 and 1874 on the moderate sites. The TTs only showed high frequencies on the dry sites in the years 1789–1793.

Only a weak positive correlation (p = 0.06) existed between the frequencies of IADFs and TTs on dry sites, whereas on moderate sites the data were not correlated (p = 0.72).

Spearman rank order correlations (Venables and Ripley 1998) between the master chronologies of stabilized IADF frequencies and climatological parameters were applied (Figure 7), as proposed by Wim-

Table 3. Descriptive statistics of sapwood and heartwood distributions. The following signif cance classes were used: [*] p < 0.05, [**] p < 0.01, [***] p < 0.001

	Dry		Moderate		K.S.Test[3]	
	Mean	SD	Mean	SD	p-value	sign
VA:						
Sapwood area[1]	320.9	104.3	586.7	165.4	0.0000	***
Basal area[1]	596.5	281.3	935.0	159.4	0.0000	***
Heartwood area[1]	275.5	163.9	348.3	82.4	0.0040	**
Sapwood rings[2]	93.6	15.9	84.7	11.4	0.0299	*
LE:						
Sapwood area[1]	237.1	114.1	555.2	169.8	0.0000	***
Basal area[1]	501.4	417.9	886.4	245.5	0.0020	**
Heartwood area[1]	264.4	221.3	331.1	148.4	0.0120	*
Sapwood rings[2]	71.8	16.8	80.2	11.2	0.2628	–
SG:						
Sapwood area[1]	192.0	88.5	604.3	231.2	0.0000	***
Basal area[1]	268.9	129.4	842.5	264.7	0.0000	***
Heartwood area[1]	76.9	52.6	238.2	61.6	0.0010	**
Sapwood rings[2]	57.9	8.8	72.4	7.6	0.0060	**

[1] $[cm^2]$ [2] Number of Sapwood rings [3] Kolmogorov-Smirnov test

mer and Strumia (1998). We used monthly values for precipitation sum, mean temperature and number of drought days as climatological parameters. A drought day was def ned as a day with <5 mm precipitation (Kuhn 1973).

The IADF frequency of the dry stands was positively correlated with precipitation in July and August and negatively correlated with August temperature. The moderate stands showed similar correlation patterns in the second half of the growing season, with positive correlations for precipitation in August and September and negative correlations for August temperature. In addition, temperature in April, June and July was positively correlated with the IADF frequency.

The correlation patterns of the number of drought days were almost the reverse of the correlation patterns of precipitation for both the dry and the moderate stands.

There were virtually no signif cant correlations between TTs and the climatic parameters.

Discussion

Ecological indicator values (Landolt 1977) are a suitable tool to compare the growth conditions of different stands. The lower humidity values on the dry sites corresponded with the higher water stress on these sites. The lower reaction values of the moderate stands, indicating more acidic conditions, were related to the higher humus values by the fact that soil acidif cation is highly inf uenced by the organic acids originating from the humus cover. The dispersion values indicated a slight tendency for reduced permeability at the moderate sites, which corresponds to the advanced status of the pedogenesis (Table 1). The light values of the dry stands were high, due to the open stand structure and to the south-exposed steep slopes where the stands were growing. The moderate stands showed lower values and the variability between the stands was high. This could be viewed in the light of differences in stand density and stand structure (Foré et al. 1997): While stand density in the VA-m stand was high and a dense understory vegetation existed, the stand structure of SG-m was open and without any understory vegetation. The differences in continentality, with lower values for the moderate sites than for the dry sites, originate in differences of stand structures and orographic positions between the stands.

Tree height, as an integrative parameter for growth conditions, clearly showed a differentiation between the site types. The dominant trees of the stands chosen as dry sites were signif cantly shorter than the trees on the moderate sites (Table 1). With comparable ages of the trees (Figure 3), these differences in tree height can be related, according to the hydraulic limitation theory (Ryan and Yoder 1997), to differences in drought stress – the smaller the mature *Pinus sylvestris*, the higher their drought stress. Because of the close relationship between water availability and nutrient regime (e.g. Larcher (1995); Scheffer and Schachtschabel (1992)), we assumed that drought stress was mostly combined with nutrient def ciencies.

Tree-ring chronologies

Diameter growth in general was higher in moderate stands than in dry stands. Growth of the dry stands was higher in only a few periods, such as 1977–1990 for site VA-d, 1860–1875 for site LE-d and 1900–1918 for site SG-d. The trees on both site types showed low growth rates, due to severe drought periods in 1894, 1921, 1944, 1947, 1949, 1976, and 1990.

Tree growth on moderate sites was balanced, characterised by higher f rst order autocorrelations, by
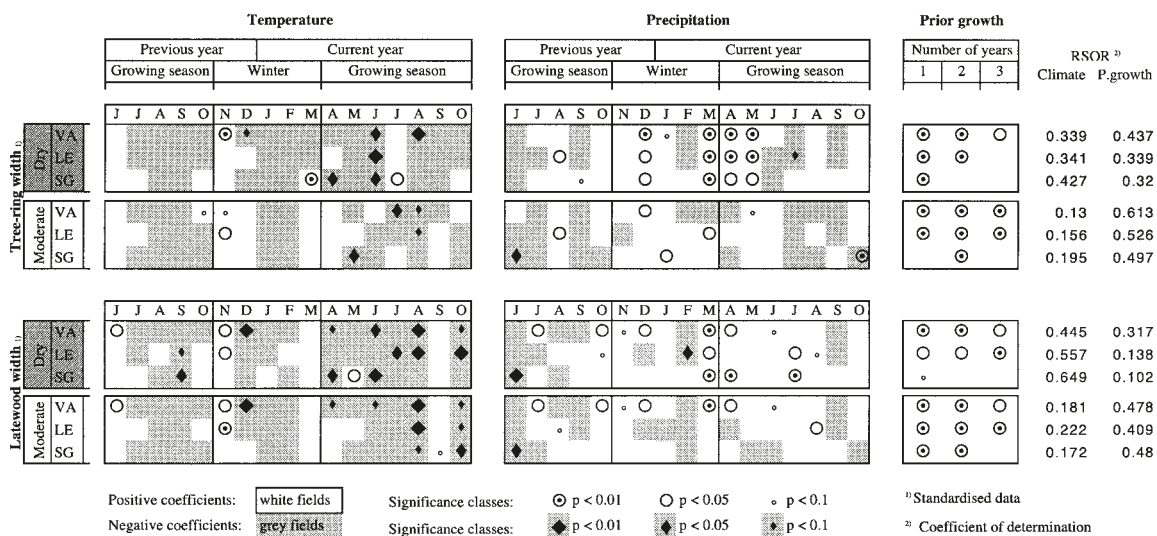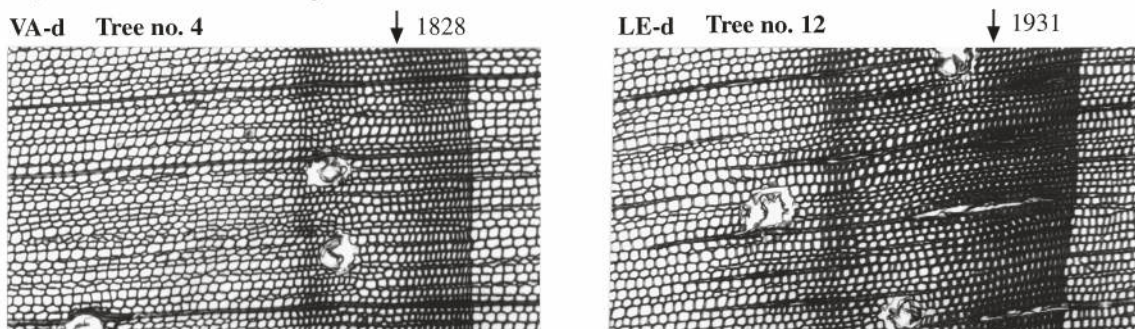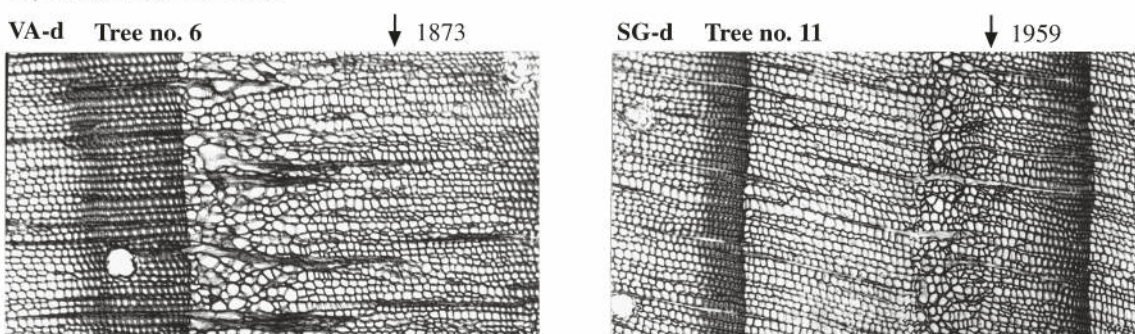
Temperature

	Previous year	Current year	
	Growing season	Winter	Growing season
	J J A S O	N D J F M	A M J J A S O

Precipitation

	Previous year	Current year	
	Growing season	Winter	Growing season
	J J A S O	N D J F M	A M J J A S O

Prior growth

Number of years			RSOR [2]	
1	2	3	Climate	P.growth

Tree-ring width — Dry (VA, LE, SG):
- 0.339 / 0.437
- 0.341 / 0.339
- 0.427 / 0.32

Tree-ring width — Moderate (VA, LE, SG):
- 0.13 / 0.613
- 0.156 / 0.526
- 0.195 / 0.497

Latewood width — Dry (VA, LE, SG):
- 0.445 / 0.317
- 0.557 / 0.138
- 0.649 / 0.102

Latewood width — Moderate (VA, LE, SG):
- 0.181 / 0.478
- 0.222 / 0.409
- 0.172 / 0.48

Positive coefficients: white fields
Negative coefficients: grey fields

Significance classes: ⊙ $p < 0.01$ ○ $p < 0.05$ ∘ $p < 0.1$
Significance classes: ◆ $p < 0.01$ ◆ $p < 0.05$ ▨ $p < 0.1$

[1] Standardised data
[2] Coefficient of determination

Figure 4. Climate response of tree-ring width and latewood width

A) Intra-annual density fluctuations

VA-d   Tree no. 4   ↓ 1828

LE-d   Tree no. 12   ↓ 1931

B) Traumatic tissues

VA-d   Tree no. 6   ↓ 1873

SG-d   Tree no. 11   ↓ 1959

Scale: ├——— 1 mm ———┤

Figure 5. Microsections of intra-annual features: A) Intra-annual density fluctuations, B) traumatic tissues. (Magnification 40-fold)

lower mean sensitivities, and by smaller numbers of missing rings. This is attributed to the balancing effect of the better water and nutrient supply due to the less extreme site conditions (Larcher 1995; Ehlers 1996). The trees may utilise more reserves, and the higher waterholding capacities of the soils (Table 1)

Table 4. Descriptive statistics of the distributions of intra-annual density f uctuations and traumatic tissues.

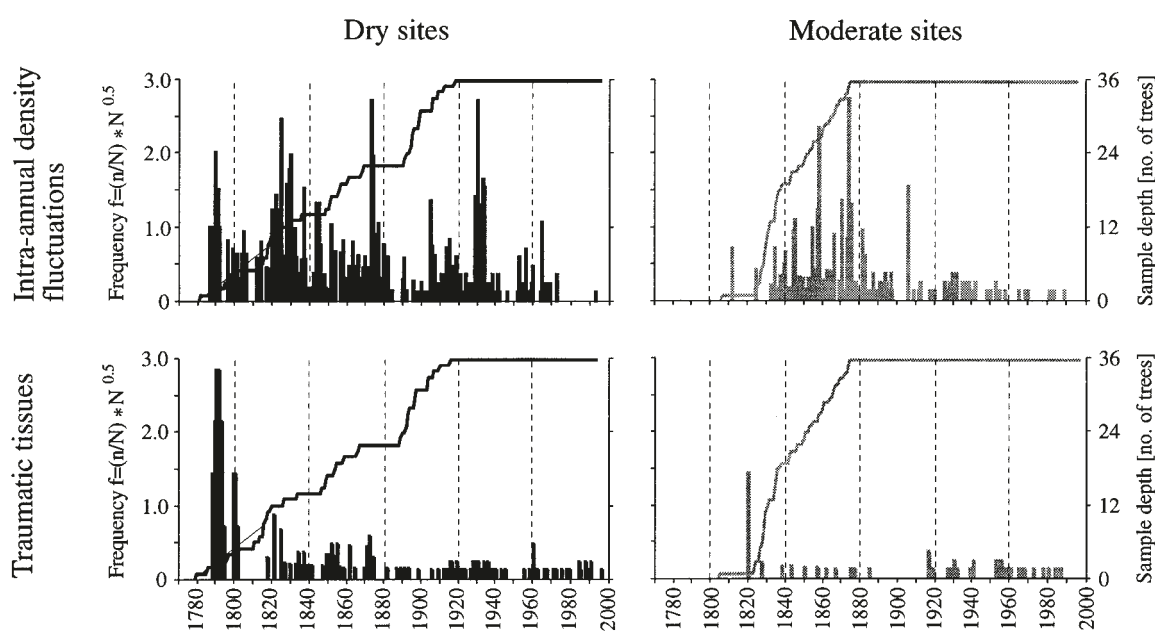|	VA-d	VA-m	LE-d	LE-m	SG-d	SG-m
Number of cores	24	24	24	24	24	24
Cores with IADF [%]	100.0	91.6	100.0	79.2	100.0	66.7
Cores with TT [%]	83.3	8.3	62.5	20.8	62.5	66.7
Rings in total[1]	3912	3850	3872	3914	2330	3280
Rings[1] wit IADF	132	99	296	108	132	49
Rings[1] with TT	57	2	40	8	48	39
Mean IADF frequency [%]	3.4	2.6	7.6	2.8	4.0	1.5
Mean TT frequency [%]	1.5	0.5	1.0	0.2	2.1	1.2

[1] Number of

Figure 6. Master chronologies of standardised mean frequencies of intra-annual density f uctuations (IADFs) and traumatic tissues (TTs) in relation to calendar years.

enable the trees to benef t from the previous year's water reserves.

Mean sensitivity was slightly increased for the dry sites, which corresponds to the results of Fritts et al. (1965) who showed that mean sensitivity increases with increasing drought stress. The moderate stands showed more low-frequency f uctuations (10–20 years), which can be related to human-induced disturbances. Growth of the moderate stands increased in 1906 (VA-m), 1951 (LE-m) and 1977 (SG-m) due to thinning (pers. com. V. Brégy, local forester). Generally, timber utilization concentrated on the moderate, better-growing sites (Rigling and Cherubini 1999; Rigling and Schweingruber 1997).

The abrupt growth increase on the dry stand SG-d after 1990 can be attributed to a forest f re. The ex-

tensive shrub-layer and the younger trees were destroyed and the surviving trees benef ted temporarily from an improved water supply due to reduced root competition and improved nutrient supply (e.g. Sannikov and Goldammer (1996); Savage and Swetnam (1990); Kutiel and Naveh (1987)).

According to de De Kort (1993), reduced vitality decreased the latewood percentage in *Pseudotsuga menziesii*. This corresponds to our results, where the earlywood-latewood ratio was increased on dry sites, signifying a reduced latewood proportion. Cell growth in general is negatively affected by water deficits (e.g. Kramer (1983); Kozlowski et al. (1991)). Therefore, the latewood proportion is reduced on dry sites with high water def cits in summer. Sapwood area is closely related to the tree's growth and its
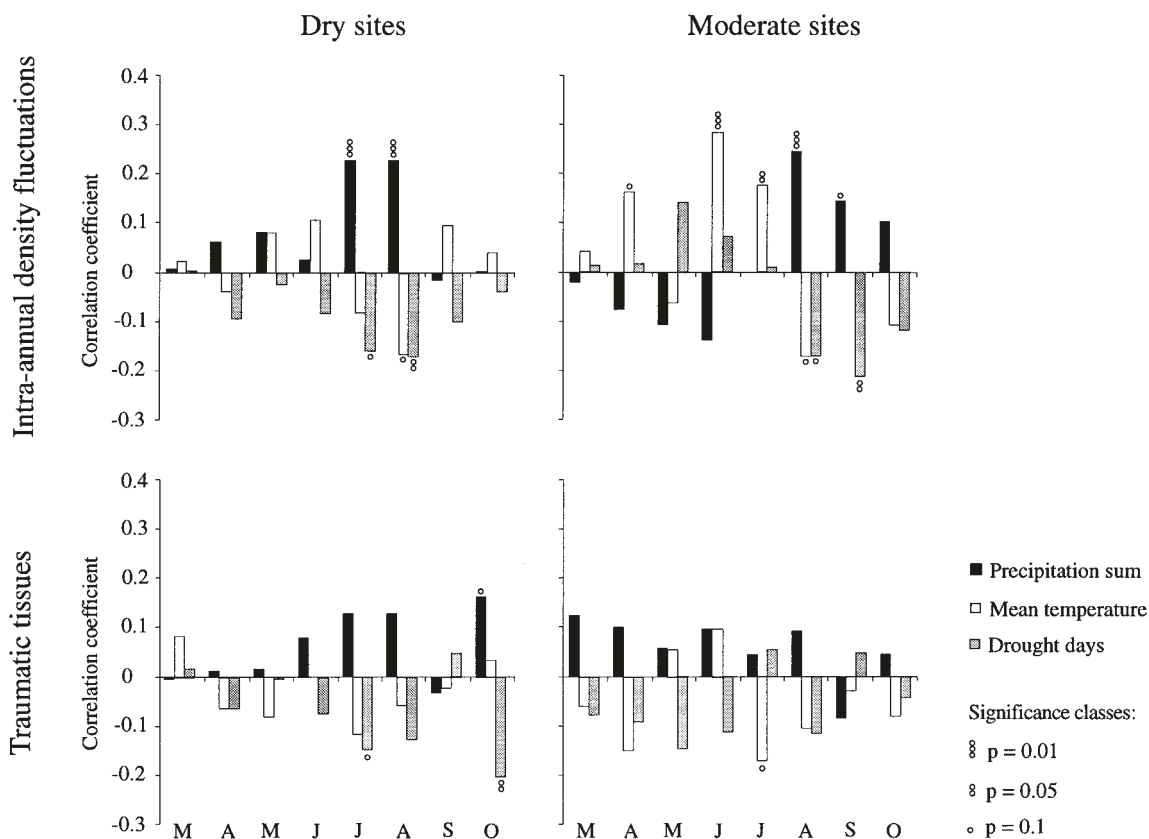
Dry sites   Moderate sites

Intra-annual density fluctuations

Traumatic tissues

Figure 7. Spearman rank order correlations between the master chronologies of standardised mean frequencies of intra-annual density fl uctuations and monthly climatic data.

physiology. Sellin (1994, 1996) showed increased sapwood areas for well-growing *Picea abies*. De Kort (1986) investigated *Pseudotsuga menziesii* of differing vitality and found reduced sapwood areas for the less vital trees. These results are conf rmed in our study, in that we detected signif cantly lower sapwood areas in the slow growing and stressed trees from dry sites than from moderate sites. In accordance with Albrektson (1984); Mäkelä and Albrektson (1992), we can show that the reduction in the sapwood areas results from a reduction in the tree-ring widths and not from the number of sapwood rings, which does not change signif cantly between the site types. Vanninen et al. (1996); Climent et al. (1993) found a negative relationship between canopy closure, stand density, and sapwood area of *Pinus sylvestris* and *P. canariensis*. Increasing canopy closure and stand density lead to a reduction in the single tree's foliage biomass. As a consequence, this leads to a decrease in the tree-ring width and a reduction in the sapwood area (Albrektson 1984). The trees seem to adjust their sapwood areas to the available amount of water in the

soil or to a reduced need of water due to a reduction in their foliage biomass by a reduction of the tree-ring widths.

Climate–growth relationships

Tree growth on dry sites was positively inf uenced by precipitation at the end of the winter and the beginning of the growing season, and negatively inf uenced by temperature in June (Figure 4). This corresponds with the results of Kienast et al. (1987) for the Swiss Alps, of Tessier (1982) for the French Alps and of Oberhuber et al. (1998) for the Inn valley near Innsbruck in Austria. Camarero et al. (1998) showed for *Pinus sylvestris* on dry sites in the Pyrenees that in the middle of July, approximately 80% of the tree-ring is already produced. The same authors suggested that a lag exists between the controlling climatic factors and ring growth. This may explain why in our study precipitation in June and July and temperature in July are of lesser importance for the formation of tree-rings.

On dry sites, winter precipitation (December and January) was positively correlated with radial growth. The frequent high temperatures during winter on the steep, south-exposed slopes can lead to high evaporation rates. Photosynthesis may take place, leading to water use, as documented for steppe vegetation (Frey 1934) and for subalpine Norway spruce (*Picea abies*) in the Swiss Central Alps (Zweifel 1999). Altough root growth during winter is mainly controlled by soil temperatures, with growth only at temperatures above 5 °C, winter precipitation may have a positive influence on dry and warm sites, where temperature is not permanently limiting root growth (Engler 1903; Santantonio and Hermann 1985; Polomski and Kuhn 1998). Since mykorrhizas are active at soil temperatures above 1 °C during winter (Vogt et al. 1980; Niederer et al. 1992; Kleinschmidt et al. 1998), winter precipitation can have a stimulating effect on growth of mykorrhizas and as a consequence on tree growth in the following spring. Furthermore, winter precipitation may control water availability at the beginning of the growing season (Lingg 1986), with important consequences for the successful beginning of root and subsequent shoot growth of the plants (Leibundgut et al. 1963; Turner and Streule 1983; Kozlowski et al. 1991).

In latewood, the pattern of the significant signals was more spread out than for earlywood, corresponding to the increased longevity of latewood cells in relation to earlywood cells (unpublished data). Depending on the time of the latewood cell formation, the climatic signals in the second part of the growing season are more apparent than in the early part of the season.

The strong negative influence of temperature on latewood growth during the growing season seems to be a characteristic of the Valais, as the *Pinus sylvestris* in the Inn valley in Austria investigated by Oberhuber et al. (1998) did not show any significant signals. This is consistent with the higher continentality of the climate in Valais in comparison to the Inn valley, as discussed by Ozenda (1988).

On moderate sites, tree growth (ring width and latewood width) was less controlled by climate than on dry sites, as indicated by the low variances explained by climate, the few significant climatic signals and the absence of a common distribution pattern of the climatic signals among the sites. Tree growth depends more on prior growth than on climate. This may confirm the above discussion about radial growth characteristics (Figure 3, Table 2).

Intra-annual features

The Spearman rank order correlations between the master chronology of IADFs and the climatological parameters showed cool-moist conditions in the middle of the growing season as determining parameters on dry sites.

In the Rhine Valley near Freiburg (310–370 m a.s.l.) and in the region of Tharandt (380–450 m a.s.l.) in Germany, radial growth of pines starts in March (Henhappel 1965; Fiedler and Wenk 1973), in the Swiss lowlands (400–500 m a.s.l.) at the beginning of April (Leibundgut 1984), in the Spanish Pyrenees (1200–1300 m a.s.l.) around end of May (Camarero et al. 1998), and at the alpine timberline in Valais (Switzerland, 1800 m a.s.l.) in the middle of May (Müller 1980). On our dry and warm sites, the pines start growing probably around April, producing earlywood cells. In a normal year, latewood production begins around July (Camarero et al. 1998), or even earlier during dry conditions (Kraus and Spurr 1961), and usually lasts until the end of the growing season. In the case of a cool-moist July and August, earlywood-like cells are produced again and interrupt the development of latewood (Figure 5), resulting in an IADF. These results are in agreement with the studies of Schulman (1938, 1939); Kuo and McGinnes (1973), also conducted on dry sites.

On the moderate sites, the determining cool-moist period is delayed by one month and lasts from August to September. This delay is consistent with the results of Kraus and Spurr (1961), who showed that the transition of earlywood to latewood in general occurs later under moist conditions. A warm period must precede the cool-moist conditions in the middle of the growing season for an IADF to be initiated. This can be related to the investigations on temperate sites by Krause (1991); Villalba and Veblen (1996); Leuschner and Schweingruber (1996); Wimmer and Strumia (1998), who all mention drought early in the growing season as a triggering factor for IADF production.

As a consequence of the additional pre-conditions, the frequency of IADFs is lower on moderate sites than on dry sites.

We failed to find a relationship between climate and TT production. The question arises as to which parameters initiate TTs other than climate. Frost can be excluded as the features were not concentrated at the time of late and early frost occurrence and because the rays did not show the characteristic bend-

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ing and enlargement described by Stöckli and Schweingruber (1996). Biotic factors such as wounding by insects or birds (Schweingruber 1996) may be responsible for the development of TTs, but this cannot be confrmed with our data.

Conclusions

Following Rolland et al. (1999), we suggest that basic phytosociological units are relevant as sampling units for investigating tree growth–site interactions. By using such units, growth dynamics of study stands can be assigned to forest communities and may be related to additional information about forest protection, silviculture, nature conservation and forest and landscape management. In addition, the use of phytosociological units to describe study sites facilitates comparison with similar studies.

Our investigations have shown that the climate response of tree growth in the generally dry *Pinus sylvestris* forests of the Erico-Pinion varies strongly. Whereas the trees of the Odontito–Pinetum on extreme dry sites are highly dependent on climate, the trees of the less, but still dry Ononido–Pinetum show a weaker relationship with climate. This suggests that dendroclimatological studies analysing the infuence of precipitation on tree growth on dry sites should focus on the most extreme sites, which implies careful site selection. The incorporation of intra-annual features into dendroecological and dendroclimatological investigations is highly recommended. It enables the distinction of site types and the characterisation of tree growth in special years with extraordinary growth conditions. The combination with the traditional climate–growth analysis using response functions increase the amount of information that can be obtained from tree growth.

Because of the correlation between intra-annual features, such as IADFs or TTs and ring width or ring age, respectively, we suggest sampling trees of all age classes in order to develop chronologies that are homogeneous over time. The analysis of intra-annual features should preferably be based on cross-sections and not exclusively on cores, as cross-sections enable the better interpretation of the features.

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