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ORIGINAL ARTICLE

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Effects of climate on vertical resin duct density and radial growth of Norway spruce [*Picea abies* (L.) Karst.]

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Abstract Vertical resin duct density in spruce tree-rings was used as a dendroclimatological variable and compared with radial growth. Resin duct density data were statistically stable and distributed with higher mean sensitivity and standard deviation but lower signal-to-noise rate than the corresponding growth rate. Radial growth and resin duct density relationships with climate were investigated using correlation and response function analysis. It was found that resin duct density has a significant positive response to above-normal temperature especially from June to August and a less significant negative response for above-normal precipitation from May–July during the current growing season. Ring width showed a significant negative response to above-normal precipitation from June to August but no response with temperature. Ring width and resin duct density were not related to each other. Sufficient data indicate that vertical resin duct density is a useful variable for dendroclimatology.

Key words Resin duct · Tree ring · Dendroclimatology · Spruce · *Picea abies*

Introduction

Many tree-ring variables can be correlated with climatic variations. These variables include ring width (Fritts 1976), earlywood and latewood widths, proportion of latewood (Oleksyn and Fritts 1991), tracheid size (Vaganov 1990), vessel size (Sass and Eckstein 1995), wood density (Cleaveland 1986; Schweingruber 1988), and chemical isotope ratios (Leavitt and Long 1991). The purpose of the present work is to investigate climatic control of resin duct density and widths of tree rings of a conifer species.

Resin ducts are a constant feature of the wood of only a few members of the *Pinaceae* family, in particular with *Larix*, *Picea*, *Pinus*, *Pseudotsuga* and *Cathaya* (LaPasha and Wheeler 1990). Duct diameters are largest in *Pinus* species (60–300 μm) and smaller in *Larix* (40–80 μm), *Picea* (40–70 μm), and *Pseudotsuga* (40–45 μm) (Larson 1994). Both vertical and radial resin ducts are found in these genera, and both types occur in traumatic as well as normal duct systems. Species of *Abies*, *Cedrus*, *Pseudolarix*, and *Tsuga* do not normally possess resin ducts. However, traumatic vertical resin ducts have been reported in *Abies* (Fahn et al. 1979; Torelli et al. 1992), *Pseudolarix* (Bannan 1936), and *Tsuga* (Leney and Moore 1977).

The seasonal timing of formation of vertical resin ducts and their incidence in relation to radial growth of the stem has been questioned for some time. Reid and Watson (1966) claimed that vertical ducts form during the latter half of the seasonal growth period. In most years resin ducts are concentrated in the outer portions of the annual ring. For lodgepole pine 88% of the resin ducts are in the last 40% of the tree-ring. Vertical resin duct formation might be influenced by external conditions (Wodzicki 1961; Larson 1994). In a laboratory experiment using 2-year-old *Pinus halepensis* Mill. Zamski (1972) showed that temperature and photoperiod changes influence resin duct formation with a time lag of several months. The study also proved temperature to be of higher importance than photoperiod. Ruden (1987) has measured ring width and resin duct frequencies in Scots pine and correlated both variables with climatic data. Generally, rather little work has been done on mature trees to show a link between the occurrence of vertical ducts and external environmental factors such as climate.

Materials and methods

The study site consisted of two established plots in the forest district Seyde, Eastern Erzgebirge, 50 km south of Dresden, Germany, close to the Czech border (Fig. 1).The plots were even-aged, approximately 80-year-old stands of Norway spruce [*Picea abies* (L.) Karst.], both

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Fig. 1 Map of the site area Seyde, Germany, in the East Erzgebirge close to the Czech border

located on quartzporphyric bedrock. The natural forest community is a mixed beech-fir-spruce forest ("Fago-Piceetum") up to an altitude of 800 m a.s.l. Spruce trees covered 80% of the area and the predominant brown forest soils are partially podsolized. The two approximately 80×80m plots had similar aspects; but they had different degrees of human disturbance because of heavy sulphur dioxide pollution from industrial facilities located to the south and east. Site A, located at 730 m a.s.l., is slightly influenced by pollution, and has a stocking density of 0.7. Crowns show 0–30% needle loss. Site B, located at 810 m a.s.l. on a ridge, is heavily affected by pollution due to its exposition and has lower stocking density (0.4) with average tree heights 20% less than on site A. Crowns of the trees on site B show needle loss of greater than 50%.

Meteorological data

The Erzgebirge is located in a transition from atlantic to continental climate types. East Erzgebirge experiences especially high fluctuations in temperature with cold winters and little precipitation. Annual total precipitation for these sites is 965 mm, 38% of which is snow. Annual mean temperature is 5.5 °C, with −23 °C as the lowest temperature measured. We used homogenized climatic data representative for the Seyde area (Deutscher Wetterdienst, Wetteramt Dresden) compiled from several stations with a minimal distance of 3800 m away from the sites and at the same altitudinal range (750 m a.s.l.). Monthly values are presented in Table 1. Cloudiness and wind are more prevalent on site B than on site A. Main wind directions are north and north-west.

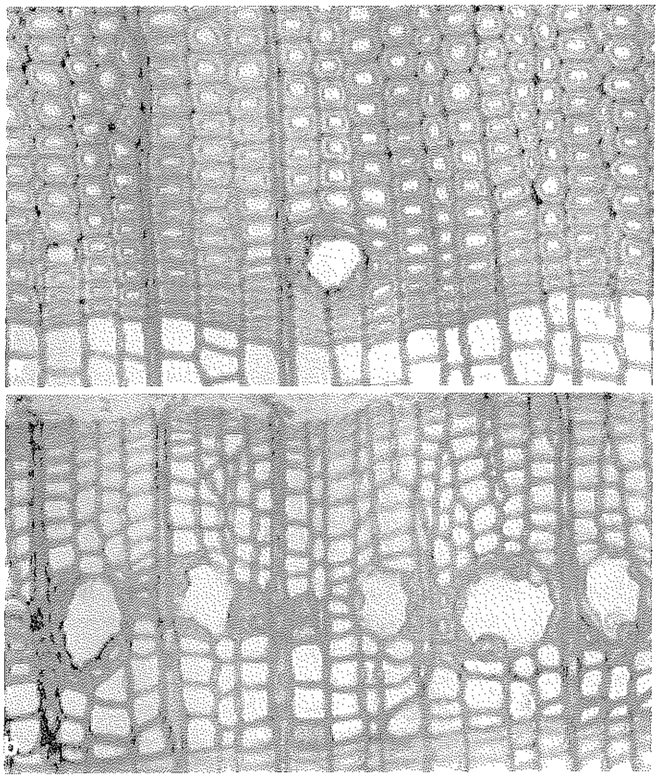

Fig. 2 Normal single vertical resin duct (**a**); traumatic vertical resin ducts formation in a recent tree ring (1991) of Norway spruce on site B (**b**). Traumatic resin duct formations were not included in the analysis

Sample preparation

In April 1993 ten dominant and codominant trees were felled on each site and 5-cm-thick stem disks were removed at 4-m tree height. Disks were immediately taken to the laboratory for the preparation of a continuous series of blocks from pith to bark. Transverse sections 20-µm-thick were cut from the blocks using a slide microtome and sections were dehydrated, stained with methylene blue and mounted in Malinol on slides (Gerlach 1984).

In a preliminary study we found in several spruce trees on site B missing rings and traumatic resin duct bands almost exclusively in the years after 1985. This is possibly linked to high air pollution levels in the studied area. According Bemmann et al. (1995) thinning in recent years has opened this site and exposed the trees to an increased concentration of gaseous sulphur dioxide, and higher wind-storm

Table 1 Monthly total precipitation and mean temperature at Seyde, East Erzgebirge, Germany, 1914–1993

	Total precipitation (mm)	Precipitation standard deviation	Mean temperature (°C)	Temperature standard deviation
January	77	46	−3.6	3.2
February	67	44	−2.8	3.4
March	69	44	0.7	2.4
April	75	41	4.9	1.8
May	82	49	10.3	1.7
June	95	55	12.4	1.7
July	113	76	15.1	1.3
August	96	57	14.1	1.3
September	69	43	11.0	1.5
October	73	52	5.9	1.6
November	70	42	0.5	1.7
December	76	49	−2.3	2.3

Table 2 Descriptive statistics for ring width and resin duct density indices for East Erzgebirge Norway spruce

	Ring width		Resin duct density	
	Site A	Site B	Site A	Site B
No. of trees	18	15	10	10
No. of radii	34	29	28	30
Mean sensitivity	0.1443	0.1558	0.7631	0.7739
Standard deviation	0.2175	0.1917	0.6554	0.6853
Skewness	−0.032	−0.7445	0.6554	0.6560
Kurtosis	−0.3639	1.0010	0.3806	0.0559
First order autocorrelation	0.68	0.51	−0.22	−0.11
Mean interseries correlation	0.42	0.38	0.24	0.28
Mean correlation between trees	0.42	0.37	0.22	0.26
Signal-to-noise ratio	12.14	8.30	2.85	3.54
Variance of first eigenvector	46.0	43.8	28.5	33.3

exposure could have caused traumatic resin duct formations in the recent tree-rings. In this study, we did not investigate air pollution effects, therefore we decided to analyze the time period between 1941 and 1987, which includes a minimum of 20 trees for the resin duct density as well as the ring width chronologies.

Resin duct measurements

Two radii, one north the other south oriented, were prepared from each disk and sections were observed using a light microscope with a CCD-camera connected to a Macintosh computer that was loaded with the NIH-Image analysis system (Wayne Rasband, National Institute of Health, USA). Resin ducts were counted in each individual ring from pith to bark for a tangential window 3.4 mm wide. Numbers were related to an area that was obtained by multiplying the given tangential window by the ring width, which resulted in the parameter "resin duct density". This parameter was independent from ring width because no relationship was found either between ring width and resin duct density ($R^2 = 0.04$, n.s.) or between ring width and plain numbers of resin ducts for a given tangential window ($R^2 = 0.14$, n.s.). We also differentiated between regular and traumatic resin duct formations, although Fahn and Zamski (1970) stated that distinction between normal and traumatic resin ducts is difficult. We did not include tangential bands of axial resin ducts that occured mostly marginally in the latewood, which we clearly considered as an anomalous (= traumatic) resin duct formation (Fig. 2). We did not include the first ten juvenile tree-rings in our chronologies because vertical resin ducts tend to be more numerous per unit area in young growth rings near the pith (Larson 1994).

Ring width measurements

A second disk was taken from each felled tree and prepared for ring width measurements. We improved the ring width chronologies by taking increment cores from an additional eight trees on each site at breast height and from two opposite directions. Cores were mounted in wooden blocks and sanded until individual tracheids were visible. All ring widths from cores were crossdated (Swetnam et al. 1985). Ring widths were measured to the nearest 0.01 mm with an incremental measuring machine and all data were checked for dating and measurement errors using COFECHA (Holmes 1983). For all tree-ring data we used a two-stage process of detrending calculated by ARSTAN (Cook 1985). First, a modified negative exponential curve or alternatively a linear regression was fitted to the raw data and second a cubic spline of a relative stiffness of 128-years was fitted to the resulting indices.

Descriptive statistics

Descriptive statistics for the measured disks and cores are presented in Table 2. Mean sensitivity is a measure of the variability between adjacent annual rings (Fritts 1976). Resin ducts have higher ring to ring variability than ring widths, which are less sensitive. Skewness indicates the degree of asymmetry and 0 indicates any symmetric distribution. The skewness is lightly positive or negative but stays close to 0, which indicates that the data show symmetric distributions. Kurtosis indicates the heaviness of the tails relative to the middle of the distribution. Kurtosis values are close to 0, which indicate normally distributed datasets. First-order autocorrelation is a measure of the influence of the previous year's growth on growth in the current year (Fritts 1976). Higher values indicate greater influence. Ring widths have positive and higher first-order autocorrelations than resin duct density which have negative coefficients, unusual relative to many other tree-ring variables. Resin duct density also shows higher ring-to-ring variabilty that causes more signal noise in this variable. We pooled data from both sites to one set because statistical results were not different for both sites and the time period analyzed.

Dendroclimatological techniques

Standard dendroclimatological techniques were employed using the program RESPO (Holmes 1994) to assess the climatic influence on resin duct formation and radial growth of Norway spruce tree-rings. First, we performed correlation analysis between monthly total precipitation and mean temperature and indexed ring variable chronologies. The climate variables were also lagged to determine whether climate during the previous growing season affect tree-ring formation of the current year. Correlation analysis is a first step for investigating possible relationships between environmental variables and tree-ring formation. Second, we used response function analysis as a more robust analysis that minimizes effects due to multicolinearity among variables representing the actual relationship between climate and tree growth (Fritts 1976). In this analysis, climatic data spanning previous August to current September are first orthogonalized, then entered into a stepwise multiple regression with the standard index chronology as the dependent variable. Any principal component with an eigenvalue greater than 1 was added to the multiple regression equation (Guiot 1990). The resulting regression equation contains the weights for each of the original climate variables. The standard error for each monthly coefficient was also calculated to determine the 95% confidence interval for each month in the response function. Any weight significantly different from zero indicated a month in which precipitation or temperature affects ring width or resin duct formation.

Results

Ring width

The correlation analysis between monthly climate data and ring width showed significant negative relationships between spruce growth and precipitation during July and August ($P < 0.05$) of the current growth year, the 2 months

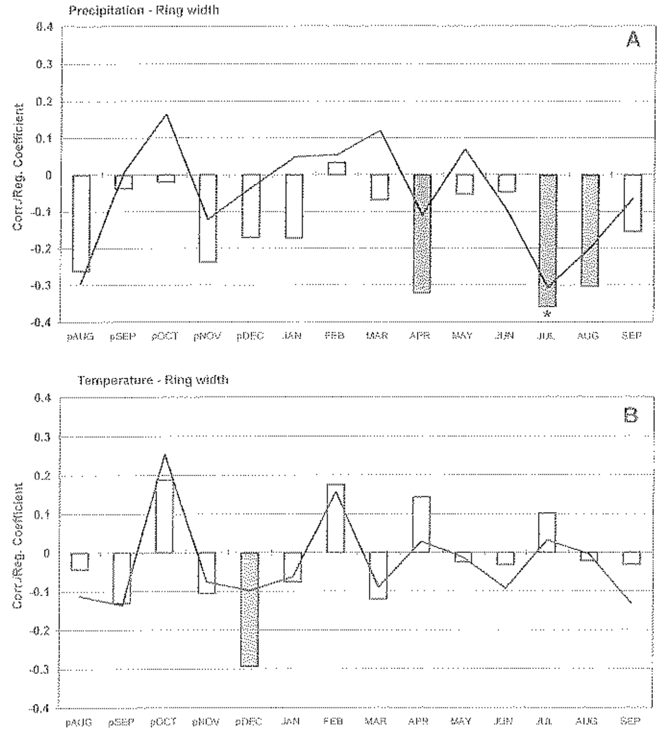

Fig. 3 a, b Results from correlation and response function analysis of Norway spruce growth in Seyde, Germany, from previous August to current September calculated for the period 1941–1987. [*Bars*: Simple correlation coefficient, significant ($P<0.05$) months *hatched*; *Line*: regression coefficients, significant ($P<0.05$) months indicated with an *asterisk*. **a** precipitation, **b** temperature]

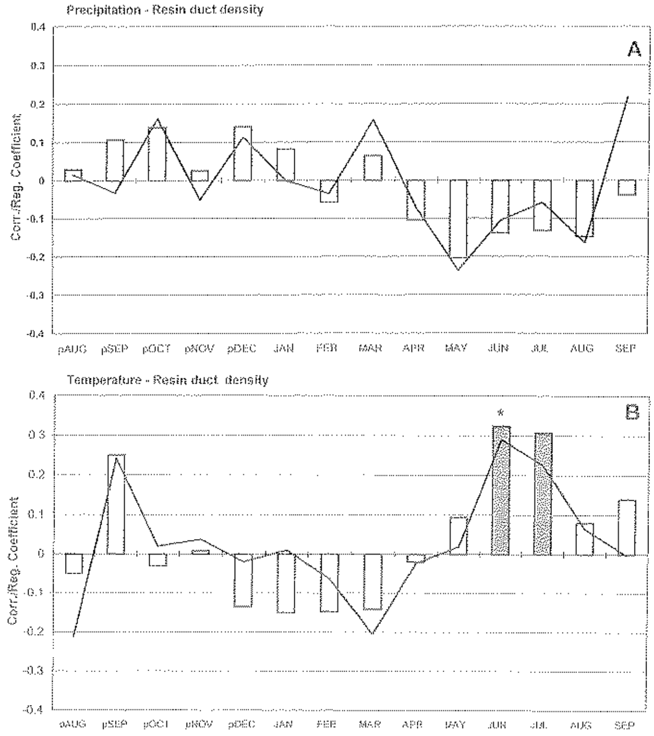

Fig. 4 a, b Results from correlation and response function analysis of Norway spruce resin duct density in Seyde, Germany, from previous August to current September calculated for the period 1941–1987. [*Bars*: Simple correlation coefficient, significant ($P<0.05$) months *hatched*; *Line*: regression coefficients, significant ($P<0.05$) months indicated with an *asterisk*. **a** precipitation, **b** temperature]

in which a substantial part of the annual growth occurs (Fig. 3a,b). April precipitation was also significant at the 5% level. A significant negative effect is also evident with mean December temperature of the previous year. Ring width significantly correlates with seasonalized total precipiation (Table 3). The strongest correlation for total seasonal precipitation occurs for the period June–August, when most of the total spruce growth occurs for this region. Temperature has relatively less effect on ring width. Using a minimum eigenvalue of 1 for entry of variables into the response function model, 20 of the 28 original components regressors were retained and explained 48% of the total variance (adjusted for loss of degree of freedom). The response function for July precipitation (Fig. 3a) showed a significant negative effect on tree growth, while temperature was not significant.

Resin duct density

Correlation analysis between monthly climatic data and resin duct density in tree-rings showed significant positive relationships with June and July temperature of the current year. A weaker, insignificant positive temperature effect is evident for the preceding September and insignificant negative effects are seen during the summer months for precipitation (Fig. 4a,b). Seasonalized climate data clearly show that temperature is the most influentual factor for resin duct density. The strongest correlation for average seasonal temperature occurs for the period June–August (Table 4). Seasonal correlations are higher than those derived with monthly precipitation and temperature data, indicating that resin duct formation can perhaps be modeled using a combination of several monthly climatic variables.

Using the same eigenvalue criterion as with ring width for the entry of variables into the response function model, 20 of the original 28 principal components regressors were retained and explained 43% of the total variance (Fig. 4a,b). Current year June temperature was positive and significant along with July which almost reached significancy as well as with the positively loaded September of the previous year. Actual and predicted yearly values are plotted in Fig. 5, along with their respective residuals as well as mean June–August temperature. The years 1975–76, 1979, 1982 and 1986 in particular reveal high resin duct densities coinciding with peaks of seasonalized June – August temperatures.

Discussion

Ring width and vertical resin duct density of Norway spruce respond to climatic variation although with some

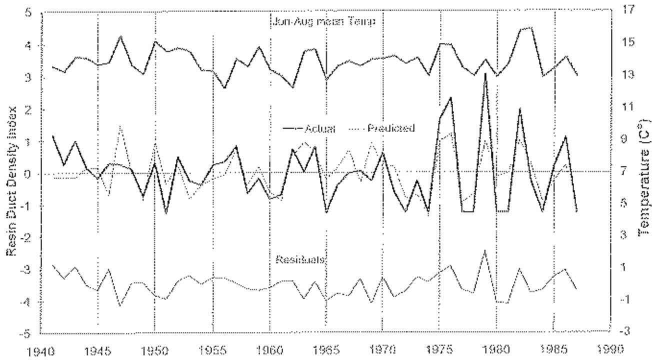

Fig. 5 Actual, predicted and residual of spruce resin ducts indices compared with June–August mean temperature

Table 3 Correlation coefficients between Norway spruce indexed ring width and intervals of the growin season (* $P < 0.01$)

Season Interval	Precipitation	Temperature
April–June	−0.210	0.134
April–July	−0.372*	0.136
April–August	−0.406*	0.150
April–September	−0.386*	0.112
May–June	−0.122	0.045
May–July	−0.358*	0.074
May–August	−0.397*	0.093
May–September	−0.374*	0.063
June–July	−0.347*	0.045
June–August	−0.410*	0.066
June–September	−0.385*	0.029

Table 4 Correlation coefficients between spruce indexed resin ducts and intervals of the growing season (+ $P < 0.05$; * $P < 0.01$)

Season Interval	Precipitation	Temperature
April–June	−0.259+	0.288+
April–July	−0.277+	0.345*
April–August	−0.262+	0.347*
April–September	−0.248+	0.344*
May–June	−0.270+	0.384*
May–July	−0.298+	0.419*
May–August	−0.274+	0.431*
May–September	−0.255+	0.400*
June–July	−0.232	0.425*
June–August	−0.229	0.443*
June–September	−0.217	0.388*

significant differences. Spring-summer precipitation significantly affects ring width in the studied area whereas summer temperature affects the formation of vertical resin ducts. Additionally, summer rain negatively affected densities of resin ducts. This indicates that resin duct formation is closely related to the seasonal climate variation and therefore could be used as a dendroclimatological variable. Few workers have investigated the relationships between vertical resin ducts and climatic factors. Reid and Watson (1966) suggested circumstantial evidence for a direct relation between high summer temperatures and large number of vertical ducts. In our study the years 1975–76, 1979, 1982 and 1986 were years with high mean June–August temperatures as well as high resin duct densities. Ruden (1987) has used resin duct frequency and ring width of seven old-grown Scots pines to reconstruct climate for a certain period. He also found resin duct frequency highly correlated with summer drought. Fahn and Zamski (1970) experimented with young saplings and adult trees of *Pinus halepensis* and showed that wounding, mechanical pressure, wind and auxins induced the formation of vertical ducts and caused an increase in the radial growth of the wood. During a later laboratory experiment Zamski (1972) reported that resin duct formation in *P. halepensis* seedlings was not synchronous with the external conditions in which the duct was formed. The ducts were always found to differentiate a number of months after cambial activity was resumed following a rest period. This probably explains why resin ducts appear more frequently in the latewood and only exceptionally in the earlywood. Werker and Fahn (1969) and Fahn (1979) found the resin ducts concentrated in the region of earlywood-latewood transition whereas Stephan (1967), Alfieri and Evert (1968), Zamski (1972) concluded that resin ducts are concentrated in the latewood. A review of pertinent literature gives the impression that vertical resin ducts are more likely to be confined to the latewood in *Pinus* than in *Picea* and *Larix*.

Our data do not show a significant relationship between ring width and number of resin ducts. Attempts have been made to correlate these two parameters but the results are equivocal. Investigators conducting quantitative studies arrived at either positive (Bannan 1936; Mergen and Echols 1955; Fahn and Zamski 1970), negative (Thomson and Sifton 1925; Reid and Watson 1966; Wimmer and Halbwachs 1992) or indifferent (Jaccard 1939) results. According to Stephan (1967), the number of vertical resin ducts increased with increasing ring width in *Pinus sylvestris*, but the density of the ducts per cm^2 of tree-ring area was greater in trees with narrow growth rings. Wimmer (1991) also found in Scots pine a negative correlation between ring width and resin duct density.

Resin duct formation is linked to growth hormones as demonstrated by a number of laboratory experiments. Fahn and Zamski (1970) have shown indole-3-acetic acid and 1-naphtyl acetic acid to be highly involved in generating more resin ducts and increasing the thickness of the radial increment. Ethylene seems to play a key role for linking exogeneous factors and resin duct formation. There are many examples of increased ethylene production following various disturbances or stress. Examples of abiotic stress include chemicals, temperature extremes, drought, hypoxia, mechanical wounding, bending, and the impedance of soil to growth (Abeles et al. 1992). Yamamoto and Kozlowski (1987) reported that ethrel – an ethylene releasing compound – stimulated an increase in the number of resin ducts in the xylem of seedlings. Many effects previously considered to be induced by auxin are possibly a result of auxin induced ethylene formation (Imaseki et al. 1982; Abeles et al. 1992), but the basic phenomenon of increased ethylene production was measured after exposure to single events of supraoptimal environmental conditions (Field 1981; Apelbaum and Yang 1981; Eklund et al. 1992). These findings do not fully explain why normal year-to-year climatic variations are linked to the formation of vertical resin ducts. Further investigations are needed to shed light on the mechanisms behind the effects of climatic variations and the vertical resin duct formation.

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