Climate response of cell characteristics in tree-rings of *Picea crassifolia*

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Abstract

Wood anatomical features measured in dated tree-rings have proven to be of value in dendrochronology. However, relatively little work has been done to define the linkages that exist between the climate signals registered in cell characteristics (cell population, diameter and wall thickness) and those in ring width or wood density. Year-to-year ring width, wood density and cell characteristics were measured at high resolution by SilviScan-3® on 30 dated *Picea crassifolia* trees growing in northwestern China. Response functions for all chronologies were calculated using dendrochronological methods. Cell wall thickness, cell population and wood density responded to temperature positively and precipitation negatively, while ring width and cell radial diameter responded to temperature negatively and precipitation positively. Cell population and radial diameter significantly responded to temperature in June and July and precipitation in August. Ring width responded to temperature in July. Cell wall thickness and wood density responded to temperature in September and precipitation in May and August. These results indicated that cell characteristics were more sensitive to climate than ring width. The more fundamental cell characteristics could be more useful in the fields of dendrochronology and dendroclimatology.

Key words: *Picea crassifolia, cell population, cell diameter, cell wall thickness, climate, dendroclimatology*

Introduction

Trees, as long-living organisms, record environmental information in their annual rings. Tree ring width and annual wood density are widely used to reconstruct climate as they can be measured easily. Improvements in digital image analysis in the last two decades have greatly enhanced our knowledge of the links between tree growth and environmental factors. The effect of factors that strongly influence stem growth are often observed within wood anatomy, as growth of tree stems is a dynamic process and influenced by whole-tree physiology (Drew et al. 2010). The importance of wood anatomy used as climate proxy was emphasized in a review on global change through investigation of the plastic responses of xylem anatomy in tree-rings (Fonti et al. 2010). The potential use of vessel features (vessel area, number, diameter and size) in hardwoods (e.g.Woodcock 1989; Sass and Eckstein 1995; Fonti and García-González 2004; Corcuera et al. 2006; Tardif and Conciatori 2006; Giantomasi et al. 2009) has revealed that vessels can be seen as climate archives with a high temporal resolution. For example, vessel size is mainly controlled by water availability at the time of cell enlargement.

It is expected that wood cell characteristics such as wall thickness, number and diameter can further reveal details of the climate signals recorded in ring width and wood density as ring width and wood density are composite properties determined largely by cell dimensions, especially in softwoods. However, only a small number of studies (Yasue et al. 2000; Wang et al. 2002; Kirdyanov et al. 2003; Panyushkina et al. 2003) have used cell characteristics in conifer tree-rings. Yasue(2000) investigated effects of the last-formed cells in annual rings on variations in maximum wood density of *Picea glehnii*, and revealed that changes in maximum wood density were due mainly to changes in cell wall thickness and not to changes in radial cell diameter. Cell wall thickness was influence positively by summer temperature and negatively by precipitation in August, and these responses were similar to those of maximum wood density. Cell number, diameter and wall thickness of *Picea Marianna* in Canada correlated with summer temperature (Wang et al. 2002), but the most important interval of the growth season when temperature influences cell production is quite short (Kirdyanov et al. 2003). For *Larix cajanderi* in northeastern Siberia, strong correlation of cell size, wall thickness and cell number with temperature was reported by Panyushkina et al (2003). They suggested that cell wall thickness and cell size may not depend on cambial age but cell number depends on cambial age does.

Picea crassifolia Kom. is an androgynous evergreen native Chinese species, with its most important populations growing in pure stands or mixed with conifer or broadleaf trees from 1700 m to 3500 m elevation of cold and semi arid regions in the northwest of China. *P. crassifolia* is the dominant species with 55.8% of the land covered by this species in the Qilian mountains (Zhao et al. 2010). The great importance of soil-water conservation of *P. crassifolia* forest in Qilian mountains was confirmed as it is the origin of the Black river, the second biggest inland river of China (He et al. 2009). A better understanding of the physiological response of *P. crassifolia* trees to climate conditions is needed, especially with respect to ongoing climate change (IPCC 2007). Three dendroclimatic studies (Wang et al. 2001; Wu et al. 2006; Peng et al. 2007) on ring width variation of *P. crassifolia* have been published. These demonstrated that ring width is mainly influenced negatively by temperature in summer.

In this study variation in ring width, wood density, cell population, radial diameter, tangential diameter and wall thickness in tree-rings of *Picea crassifolia* was measured to (a) determine the linkage of the climate signals registered in cell characteristics and those in ring width and wood density; (b) better understand the microstructural basis of ring width and wood density variation, the most popular variables used for dendrochronological and dendroclimatological research.

Materials and Methods

Study area

The selected study area is a 300 ha woodland of semi-natural *P.crassifolia* (2500-3500 m a.s.l.) in pure stands located on the north and northwest slopes of the Qilian mountains at the margin of the Tibetan plateau 48 km south of the city of Zhangye, Gansu province in northwestern China (38°32′ N, 100°18′ E). The soils in the forest were sandy loams with abundant lichens, a few shrubs and grass, and a mean density of approximately 300 trees ha^{-1}. In this region the climate is continental, strongly influenced by the desert and the Tibetan plateau. Climatic data were obtained from the Qilian meteorological station (38°11′ N, 100°15′ E; 2787 m a.s.l.) for the period 1957–2009. The mean annual temperature is 1.0°C. January and December are the coldest months in the study area, with a mean minimum temperature of –24.5°C, and the warmest is July with a mean maximum temperature of 22.1°C (Fig. 1b). The ground is usually covered by snow from mid-November to mid-April. The mean monthly rainfall ranges from almost 0 mm in January to 90 mm in July, mean annual precipitation is 338 mm, of which 85% falls from May to September with high year-to-year difference (Fig.1a).

Sample processing and measurement

Two cores from each of forty dominant *P. crassifolia* trees of similar diameter on the north slope were sampled at the study site (38°32′41″N, 100°18′25″E, 2600 m a.s.l.), by removing a 12-mm diameter, pith to bark increment core at breast height in early September 2009. Sixty cores (thirty trees) without fungi and nodes were measured by SilviScan-3® at CSIRO, Australia (Table 1).

The sixty core samples were cut using a twin blade saw to form 2 mm wide (tangential dimension), 7 mm high (longitudinal dimension) and pith-to-bark (radial) strips, and extracted with heated acetone for 48 hours to remove the influence of resin on wood density. One transverse cross-section of each pith-to-bark strip was polished sequentially using abrasive paper of 400, 800, 1200 then 1500 mesh to reveal the cell details (Fig. 2). The strips were equilibrated to a constant moisture content in a controlled environment room (temperature=20°C and relative humidity=65%) for two days.

The radial strips were then scanned in two stages after the measurement of their mass, length and width. Firstly, automated microscopy and image analysis (fifty times magnification) of the polished cross-sections gave growth-ring boundary orientation, mean radial and tangential diameter in sequential 0.025 mm (radial)×1.3mm (tangential) areas, and cell population (number of cells per square millimeter). The strip sample was then analyzed using an automated x-ray scanning densitometry system with sample rotation to maintain the x-ray beam direction parallel to the ring boundaries with resolution of 0.01 mm. The wood density profile was binned from 0.010 mm to 0.025 mm intervals to match the cell diameter profile. Cell wall thickness was calculated from tracheid diameter and wood density data (Evans 1994; Evans et al. 1995). Annual ring boundaries were generally recognizable in the cross-section images (e.g. Fig.2), and by the large, rapid drop in wood density going from latewood formed at the end of one growing season to the earlywood of the next growing season.

Data analysis

Ring width series of each sample obtained from the SilviScan-3 data were cross-dated using the COFECHA program. Each series of ring width, wood density and cell characteristics was standardized using the ARSTAN program (Cook and Holmes 1996). The ring width series were fitted to spline functions with a 50% frequency response of 32 years (Cook and Peters 1981). Wood density and cell characteristics series were fitted to negative exponential curves as there was an apparent decreasing or increasing trend in them until age of 25 years.

The indices of tree-ring variables for individual series were averaged by calculating robust biweight means, which were standardized chronologies. The statistical quality of the chronologies was accessed using standard basic statistics (Briffa and Jones 1990; Fritts 2001): the mean correlation between trees (R_{bt}), the expressed population signal (EPS), the mean sensitivity (MS) and the first-order autocorrelation (AC1).

The growth-climate relationships for the period 1957–2008 were calculated by taking the monthly mean temperature and precipitation records as climatic predictors, and the standardized index chronologies as the dependent variables. The temporal window for climatic predictors was taken from October of the year before ring formation to October of the year of ring formation. Response function analysis was used to estimate the variation in the wood indices with multiple regression, after extracting the principal components of the climatic predictors to avoid intercorrelations between them (Fritts 2001). Calculations were performed with the program PRECON (Fritts et al. 1991), which includes a bootstrap procedure to assess the statistical significance of the regression coefficients. The significance of each regression coefficient was provided by the ratio between the average value estimated from the result of 1000 simulations and its standard deviation. When the ratio ($|r/sd| \geq 2.00$, or ≥ 2.58, the significance of the corresponding regression attains 95% or 99% probability, respectively.

Results

Chronologies

Standardized chronologies of individual indices with mean indices of ring width, wood density and cell characteristics were showed in Fig.3. Table 2 gives the general chronology statistics of tree-ring variables. Mean sensitivity (MS) of ring width series was higher relative to that of wood density and cell characteristics series. The first-order autocorrelation ranged from 0.44 to 0.84 indicating that conditions influencing ring formation in one year tend to carry over their effect to the growth of the following year. The highest correlation between trees (R_{bt}) was cell radial diameter (0.71) and the lowest one was cell tangential diameter (0.09). Ring width also had quite a high correlation (R_{bt}=0.65). The correlation between wood density and cell population was higher than that between wood density and cell wall thickness. The high correlation indicates good cross matching between trees. The signal to noise ratio (SNR) and the variance explained by the first principle component (PC1) displayed similar patterns among tree-ring variables as R_{bt}. In general, higher mean sensitivity (MS), the variance explained by the first principle component (PC1), and signal to noise ratio (SNR) are believed to indicate a greater climatic influence on tree growth (Cook and Kairiukstis 1990). But this may not be true for comparisons of ring width with cell characteristics as cell radial diameter showed the highest PC1 (72.1%) and SNR (126.94) but quite low MS (0.07). In addition, the curves of cell tangential diameter were almost random and very small common signal (R_{bt}=0.09, PC1=17%, SNR=5.26), therefore it was not useful to do correlation analysis between cell tangential diameter and other tree-ring or climate variables.

Correlations between the different tree-ring variables

Spearman correlation coefficients between different raw tree-ring variables in period 1957-2008 (Table 3) displayed highly significant differences between the chronologies. Wood density significantly correlated with all cell characteristics. The correlation of wood density with cell radial diameter was negative and positive with cell population and cell wall thickness. The correlation between ring width and cell characteristics was weaker than the correlation between wood density and cell characteristics. Cell radial diameter correlated strongly with cell population (r=-0.86).

Climate response analysis

The variance explained by climate revealed different climatic sensitivity among ring width, wood density and cell characteristics. Cell population, cell radial diameter and wood density chronologies have much stronger response to climate than ring width. Climate explained 50.8% of the variation of cell radial diameter, 50.2% of cell population, 47.8% of wood density, 39.6% of cell wall thickness and 37.0% of ring width (Table 4).

The response function analysis showed that *P. crassifolia* growth was mainly influenced by temperature (Fig. 4). Ring width exhibited a significant negative response to temperature in July ($p<0.05$). Compared to ring width, wood density was more sensitive to temperature, having a positive response to temperature in July ($p=0.05$) and September ($p<0.01$). Cell population and radial diameter responded significant to temperature in June and July. As cell population and radial diameter negatively correlated with each other, cell population responded positively and cell radial diameter responded negatively.

Ring width did not show any significant response to precipitation. Wood density and cell wall thickness displayed a significant negative response to precipitation in May and August, and a significant negative response of cell population to precipitation in January ($p<0.05$) and August ($p=0.05$). Response of cell radial diameter to precipitation in August ($p<0.05$) was positive and in September ($p=0.05$) was negative.

In general, wood density, cell wall thickness, cell population and wood density as a group responded to temperature positively and to precipitation negatively, and ring width and cell radial diameter were in another group that responded to temperature negatively and to precipitation positively.

Discussion

Temperature during the growing season appeared to be the main climatic variable controlling growth, which was consistent with other results found for *P. crassifolia* trees (Wang et al. 2001) and *Sabina przewalskii* (Liu et al. 2006) in a similar climatic region. Bud break of *P. crassifolia* tree in study area starts in the middle of March and ends in early June, with stem growth being of lower priority than bud formation and root growth (Eilmann et al. 2009). The main radial growth of the stem occurs from June to September (Liu 1992) similar to that observed by Deslauriers 2003. Cell differentiation is generally agreed to commence following a period of warmer weather in which the temperature sum over a period of days exceeds a given threshold (Fritts et al. 1999). June-July is likely to be the main period for cell division and cell enlargement of *P. crassifolia* trees in the study area, and cells formed in this period largely determined the ring width as cell population, cell radial diameter and ring width significantly responded to temperature in this period.

After a cell has been produced by cell division in the cambium, it grows in the radial and longitudinal directions, and then secondary wall formation (Gindl et al. 2000). Cell number is determined by the process of cell division that is the earliest stage of differentiation, driven by a cycle of cell enlargement to a critical threshold, followed by division to generate two daughter cells (Frrits et al. 1999).The phase of cell enlargement stars as cells exit the zone of cell division (Plomion et al. 2001), which is understood to occur when the cell expansion drops below a given threshold rate (Frrits et al.1999). Delays in the commencement of cell formation leading narrow ring are commonly observed, as the beginning of the growing season varies considerably, depending mostly on climate variation (eg. Creber and Chaloner 1984; Vaganov et al. 1994). Temperature represents the most important critical factor at the beginning of the growing season, when sufficient water reserves are available. Cambial activity may be influenced by both these factors at any time of the growing season, the higher intensity of one of them always being decisive (Horacek et al. 1999). For scots pine, the temperature influenced the initial division and radial cell expansion mainly in May-June, while the influence of precipitation increased in July-August. Throughout all seasons it was the temperature that had the main influence on the biomass accumulation in cell walls (Antova and Stasova 1993). Strong correlations between temperature and ring width varied from June to August in three studies (Wang et al. 2001; Wu et al. 2006; Peng et al. 2007) of *P.crassifolia* in Qilian mountains. The significant response period of cell population and cell radial diameter was in June -July before the significant response time of cell wall thickness in this study. Wood density, involoves the whole processes of cell differentiation, and is significantly correlated to cell number, radial diameter and wall thickness. Ring width is a measure of the sum of a growing season's cell division (i.e. cell number) and cell enlargement activity (i.e. cell radial diameter) in the xylem (Gindl et al. 2000). Climate conditions that have influence on ring width and wood density should be more clearly in the component cell characteristics.

Cell characteristics were more sensitive to climate than ring width and contained different kinds of information. In the study described here the relationships between cell population, cell radial diameter and temperature were varied. Many of these effects can be best understood in terms of the interactive effects of climate on tree biology. Raison et al. (1992) and Benson et al. (1992) investigated the phenology of foliage and stem growth in radiata pine and reported that the current seasons foliage mass was due in part to the number of needles set during the previous season and the final length of the needles defined by current season spring conditions. Similarly Lanner (1976) argued that shoot development in pines is influenced by the number of needle primordia set. Together these factors define in large part, not only the amount of photosynthate available for growth but the magnitude of the hormone flux that drives cell division (Fritts et al. 1999; Drew et al. 2010). The beginning of cell formation is supported by the mobilization of reserves stored during the previous growing season (Barbaroux & Bréda, 2002). Moreover, the onset, duration and cessation of cell wall formation are important for the carbon balance of a tree because wood formation represents a large carbon sink. During cell maturation, trees allocate more photosynthate to the production of cellulose microfibrils that contribute to the building of secondary cell walls (Hansen et al. 1997). With monthly temperature going down to 8°C in September at the study area, energy produced by photosynthetic activity decreases and fructification of *P. crassifolia* occurs between September and beginning of October (Liu 1992).

Ideally the combined effects of temperature on ring width, wood density and cell characteristics need to be interpreted in terms of the phenology of growth (Downes et al. 2002). Increases in spring temperature combined with adequate rainfall and foliar growth can be expected to increase earlywood proportion with a consequent tendency to decrease annual density, increase ring width and cell numbers. This can occur because of changes in the duration of earlywood formation (Deslauriers et al. 2003) or from increases in rates of cell production per day. Similarly good growth conditions after needle elongation stops (e.g. good rainfall and warm temperatures) can be expected to increase latewood proportion with a consequent tendency to increase annual density as well as ring width and cell numbers.

Conclusion

Cell wall thickness, cell population and wood density were in one group that responded to temperature positively and to precipitation negatively, and ring width and cell radial diameter were in another group that responded to temperature negatively and to precipitation positively. Cell population and radial diameter significantly responded to temperature in June-July and to precipitation in August. As cell population and cell radial diameter, ring width also responded to temperature in June-July. Cell wall thickness and wood density responded to temperature in September and to precipitation in May and August. Cell characteristics of *P.crassifolia* contain an ecophysiological signal that can be used as a climate proxy. For these promising reasons, the cell characteristics should be further investigated at high resolution to understand the mechanism behind tree growth-climate relationships, making it possible enhance dendroclimatic reconstructions and produce higher quality wood under a changing climate.

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Table 1 Information of *P. crassifolia* trees used in this study

Number of trees/cores	Age (year)	Age range (year)	DBH (cm)	DBH range (cm)	Height (m)	Height range (m)
30/60	73.8(19.6)	57-114	28.2 (2.9)	21.8-34.2	12.6 (1.5)	9.5-16.1

Values are means (standard deviation) , Diameter at breast height(DBH).

Table 2 The chronology statistics of tree-ring variables. Mean sensitivity (MS) and first-order autocorrelation (AC1) were calculated by the ARSTAN program for the common period (1957-2008) of raw series from 52 cores (26 trees). Mean between-tree correlation (R_{bt}), the variance explained by the first principle component (PC1), signal-to-noise ratio (SNR) and expressed population signal (EPS) were calculated by ASTAN program for the same period using standardized series.

	Ring width	Wood density	Cell wall thickness	Cell radial diameter	Cell tangential diameter	Cell population
Mean/SD	1.64/0.96	0.38/0.05	2.05/0.26	31.59/2.85	31.23/2.90	1071/180
Range	0.05-7.73	0.25-0.64	1.37-3.68	22.3-38.4	23.7-40.9	607-1844
MS	0.34	0.09	0.08	0.07	0.04	0.08
AC1	0.63	0.48	0.44	0.57	0.84	0.80
R_{bt}	0.65	0.42	0.30	0.71	0.09	0.39
PC1(%)	66.5	46.1	34.6	72.1	17.0	42.7
SNR	98.66	37.32	23.15	126.94	5.26	34.19
EPS	0.99	0.97	0.96	0.99	0.84	0.97

Table 3 Spearman correlation coefficients between different tree-ring variables.

	Ring width	Wood density	Cell radial diameter	Cell population
Ring width	1.00			
wood density	- 0.28*	1.00		
Cell radial diameter	0.15	- 0.69***	1.00	
Cell population	0.28*	0.55***	-0.86***	1.00
Cell wall thickness	- 0.59***	0.64***	-0.05	-0.23

* represents significant at p=0.05. ** represents significant at p=0.01. *** represents significant at p=0.001. n=52

Table 4. Main statistics of response functions of cell characteristics , ring width, and wood density to mean monthly temperature and precipitation.

Chronology	Variance explained by response function(%)	Variance explained by climate(%)
Ring width	56.8	37.0
Wood density	61.5	47.8
Cell radial diameter	63.1	50.8
Cell population	60.6	50.2
Cell wall thickness	46.8	39.6

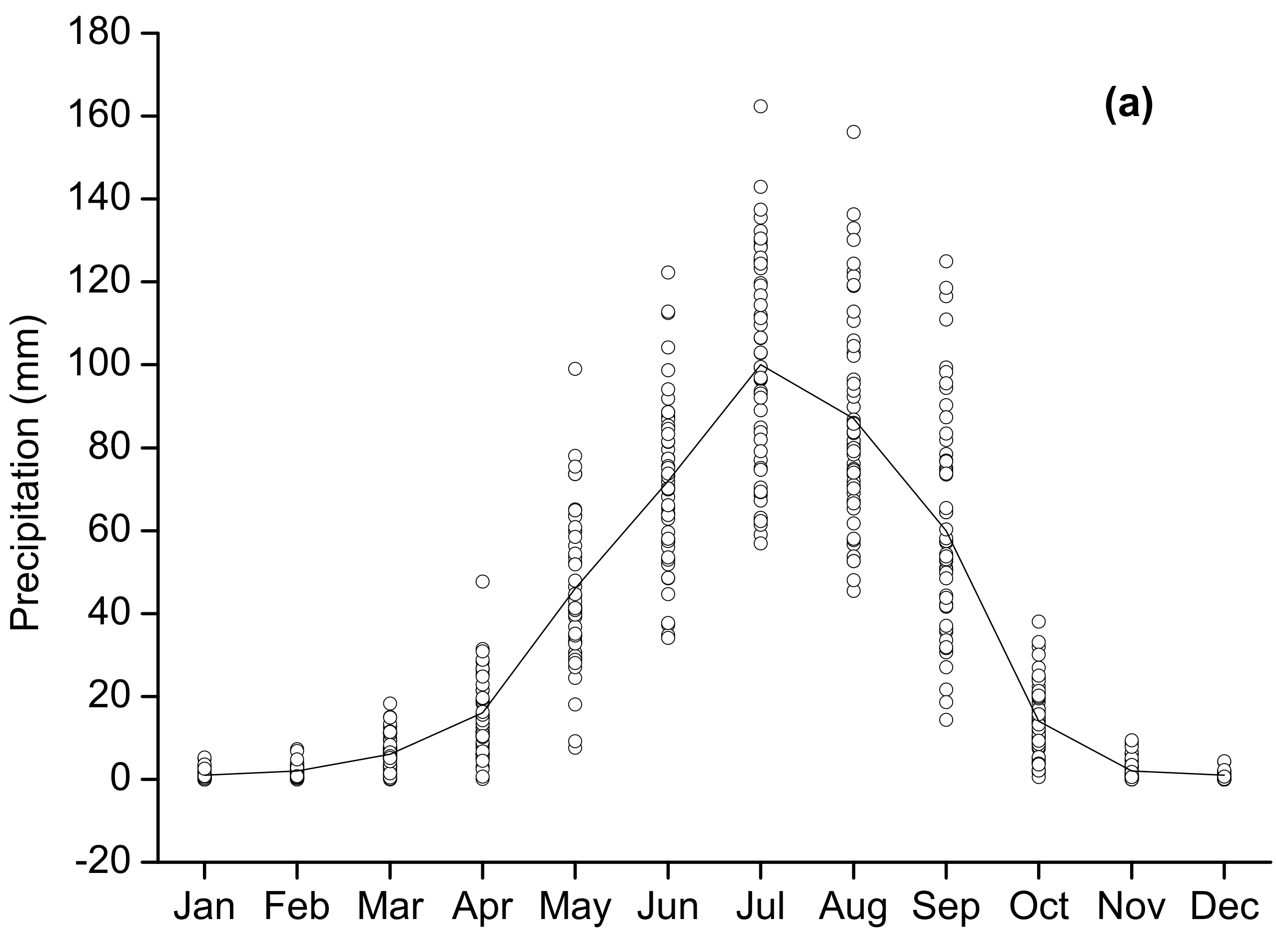
Fig.1 Climatic diagrams from the Qilian meteorological station for the period 1957-2009. The distance between the study site and the meteorological station is 30 km. (a) line indicates mean monthly precipitation, open circles indicate precipitation in each year in given month. (b) Mean monthly maximum (T_{max}), mean (T), and minimum (T_{min}) temperatures.

Fig.2 Common image from SilviScan-3® system showing the structure of a cross-section of the wood of *P.crassifolia.*

Fig.3 Time series of ring width (a), wood density (b), cell radial diameter (c), cell population (d), cell tangential diameter (e) and cell wall thickness (f) indices for the common period 1957-2008. Black bold lines indicate average chronologies; other lines show individual trees.

Fig.4 Response functions of ring with (RW), wood density (DEN) and cell characteristics(CNO=cell population, CDR=cell radial diameter, CWT=cell wall thickness) to mean monthly precipitation, Mean monthly temperatures in the period 1957–2008 expressed as regression coefficients divided by their bootstrapped standard deviations (r/sd). Dot lines indicate the significance thresholds (P = 0.05 and 0.01) for the r/sd values.

Fig.1 a



(a)
Precipitation (mm)
180
160
140
120
100
80
60
40
20
0
-20
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Fig.1b

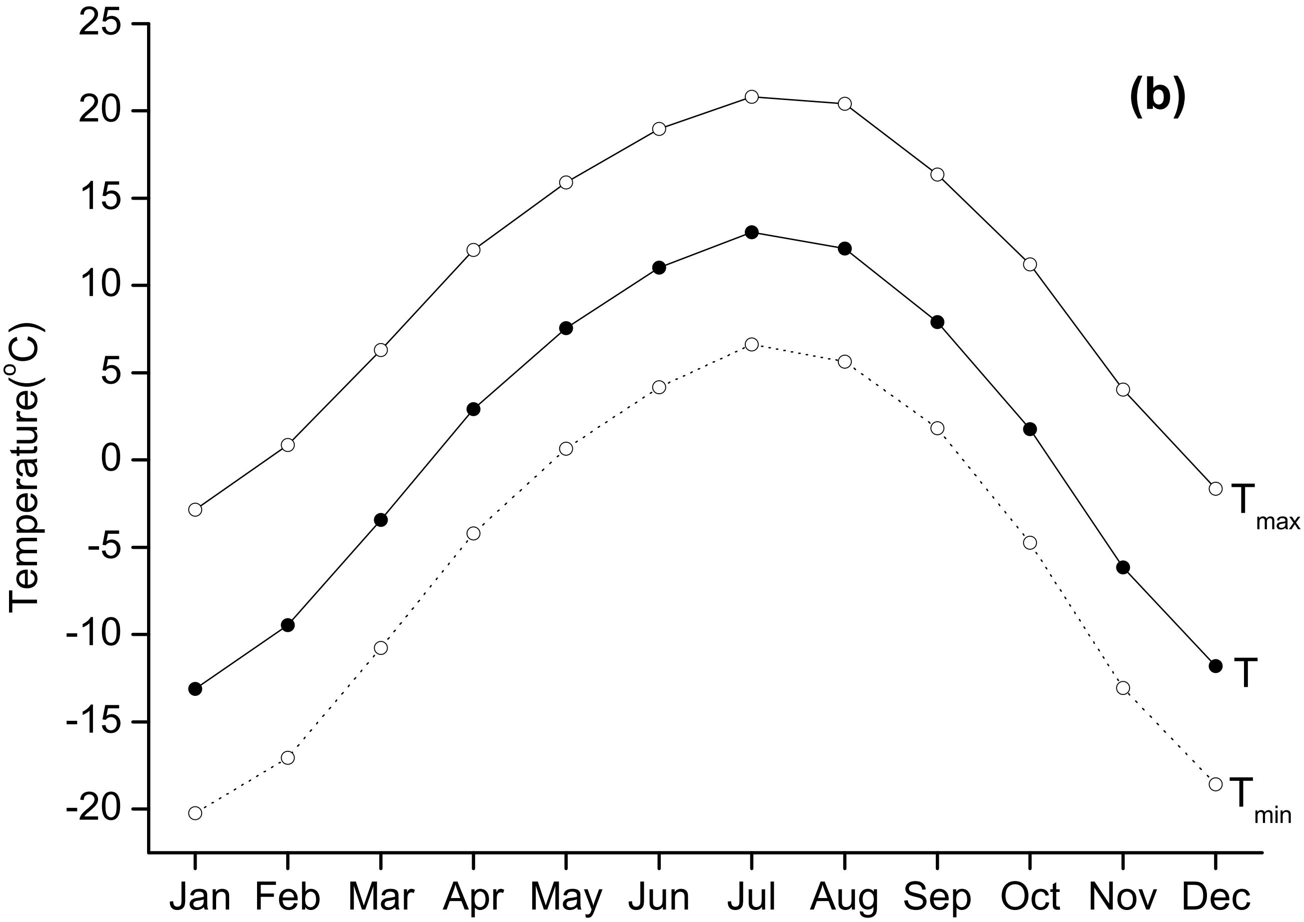

(b)
Temperature(°C)
25
20
15
10
5
0
-5
-10
-15
-20
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
T max
T
T min

Fig.2
Click here to download high resolution image

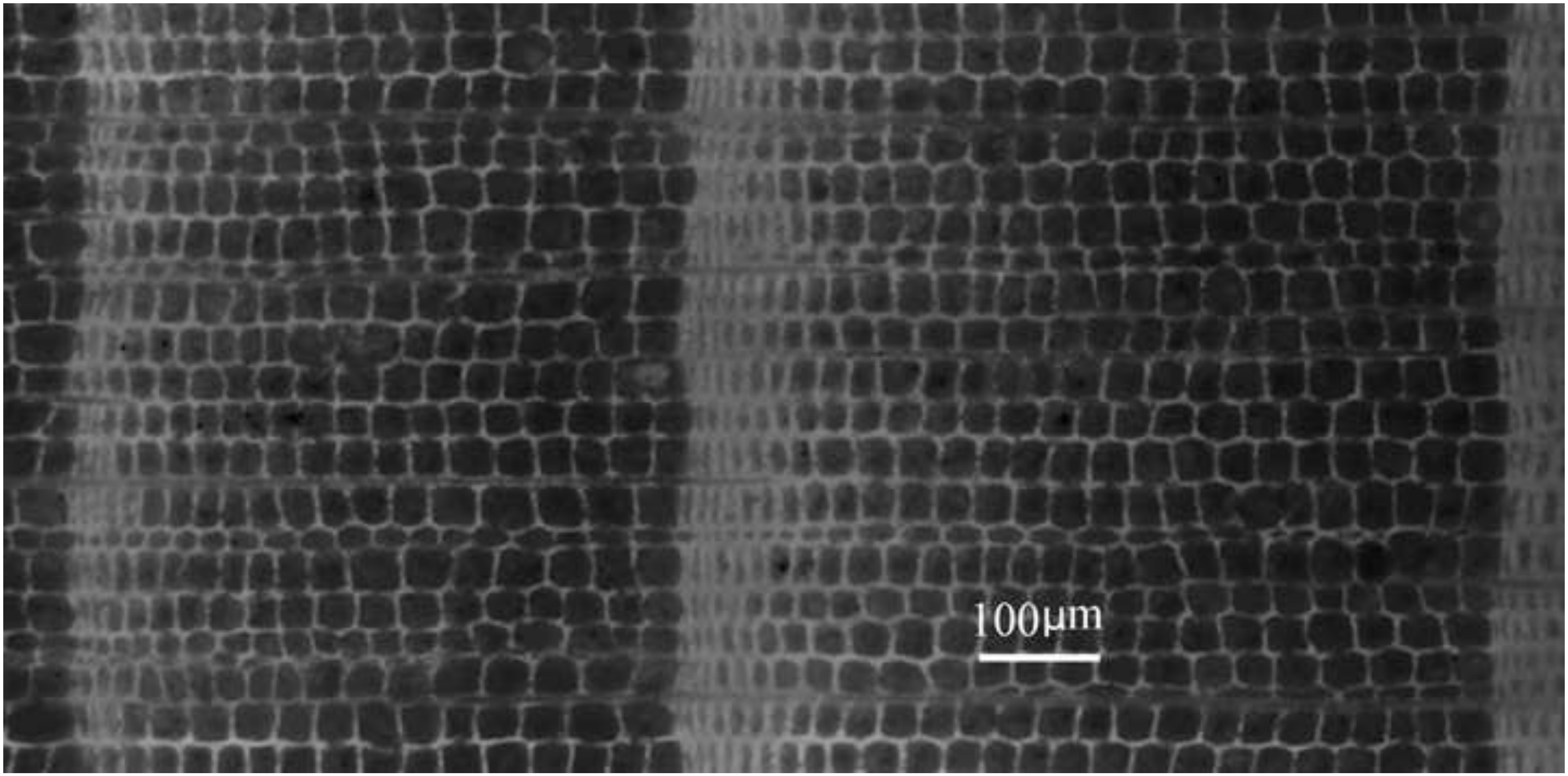


Fig.3a

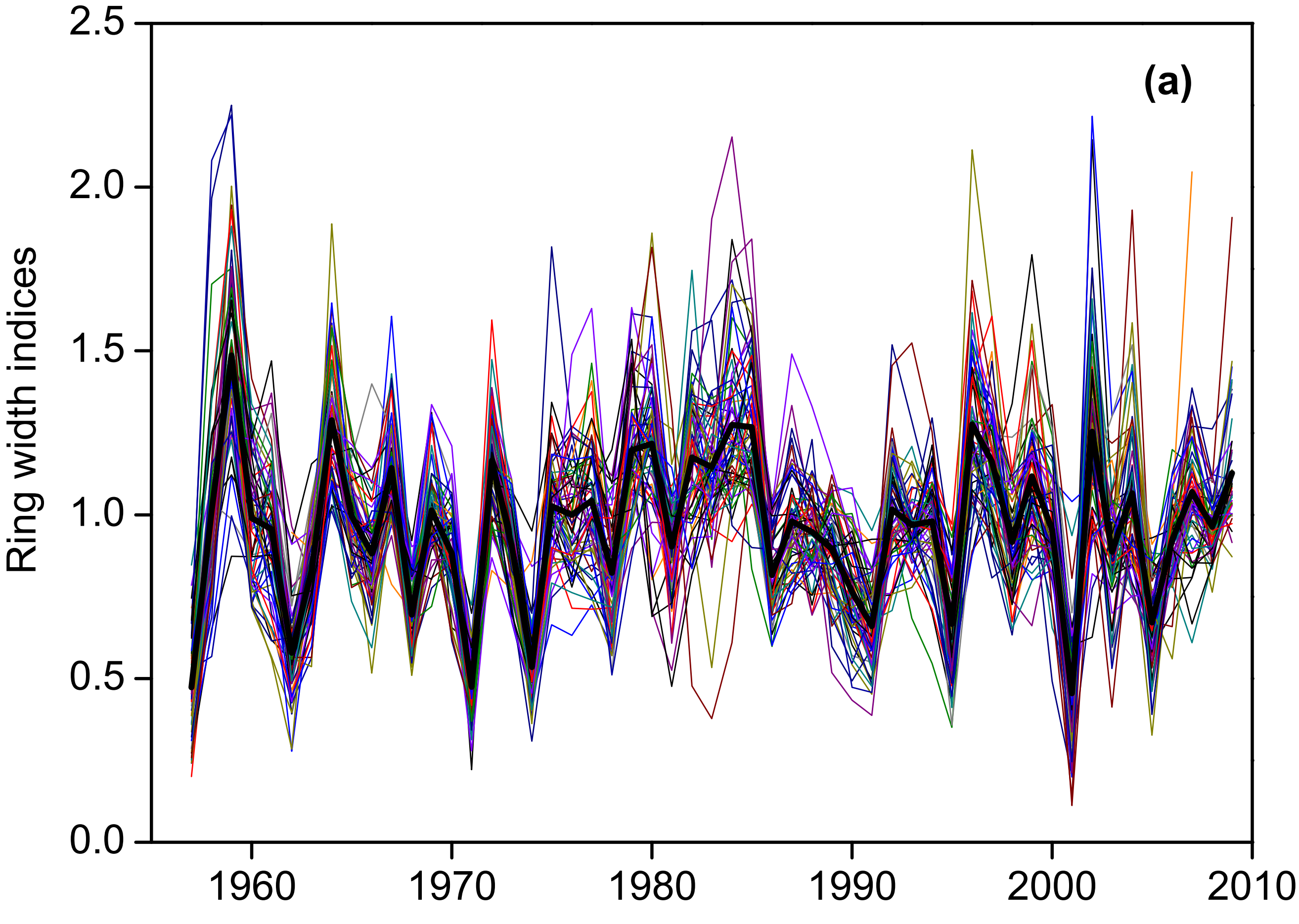
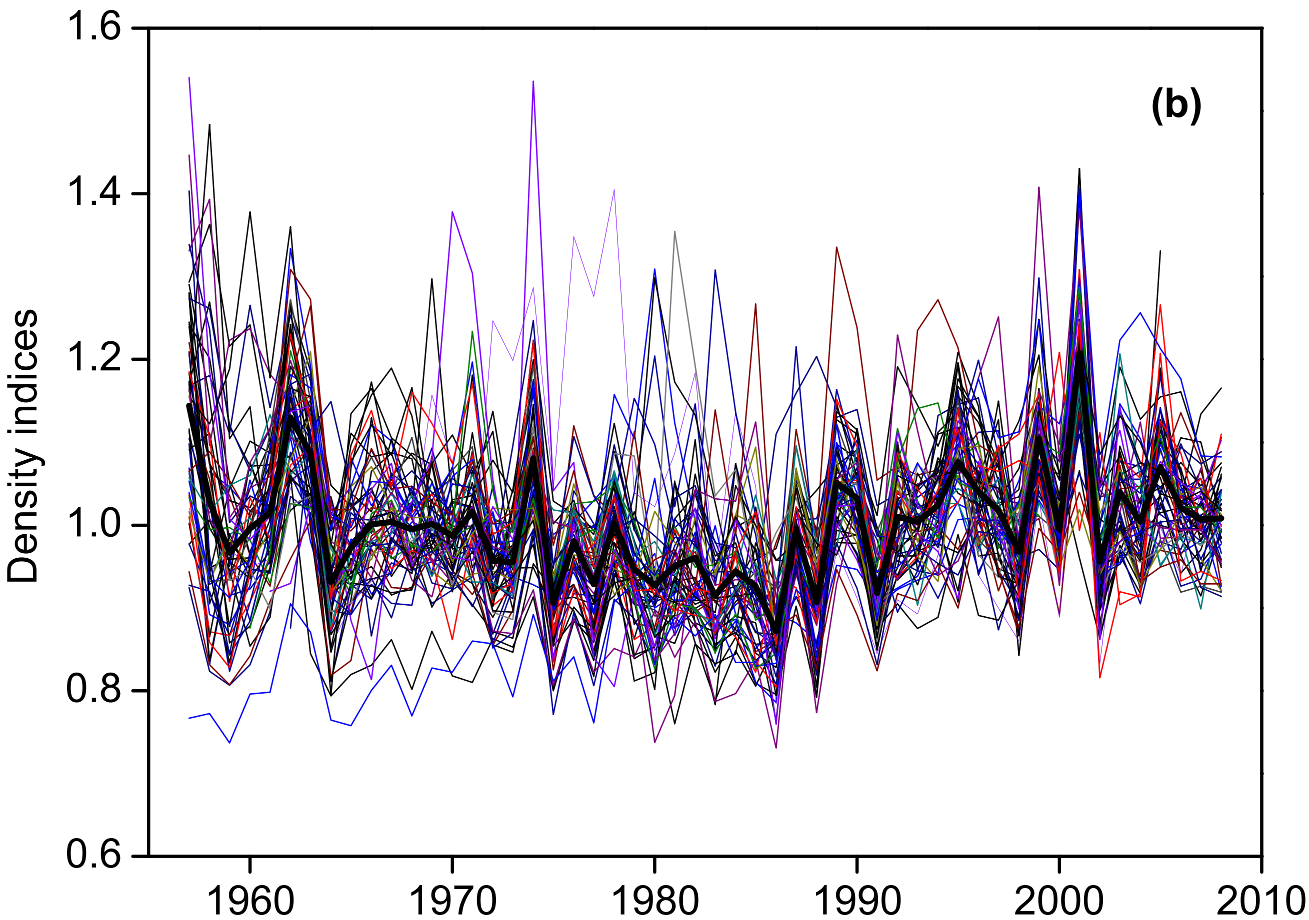

(a)
Ring width indices
2.5
2.0
1.5
1.0
0.5
0.0
1960
1970
1980
1990
2000
2010

Fig.3b



(b)
Density indices
1.6
1.4
1.2
1.0
0.8
0.6
1960
1970
1980
1990
2000
2010

Fig.3c

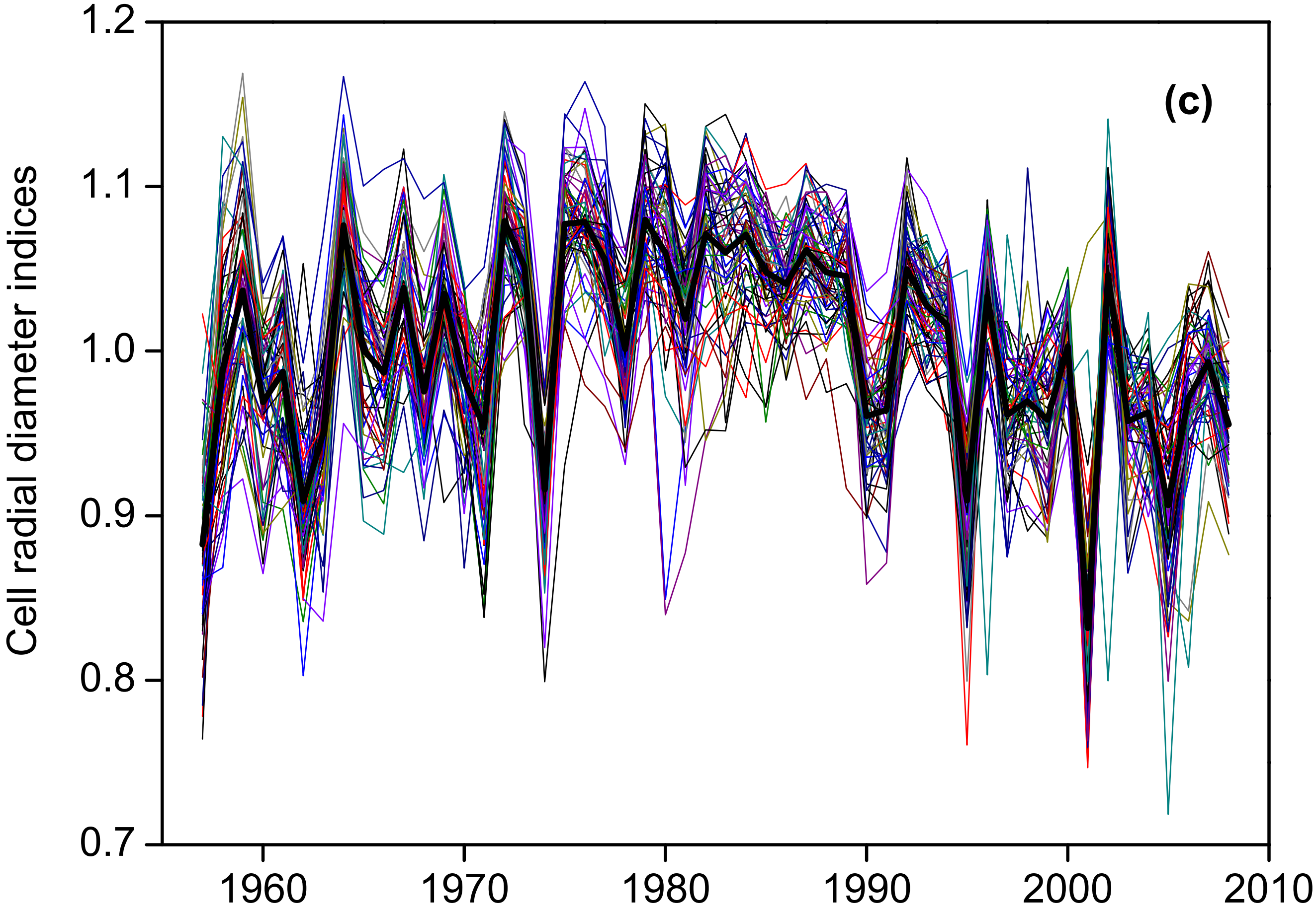

1.2
1.1
1.0
0.9
0.8
0.7
Cell radial diameter indices
(c)
1960
1970
1980
1990
2000
2010

Fig.3d

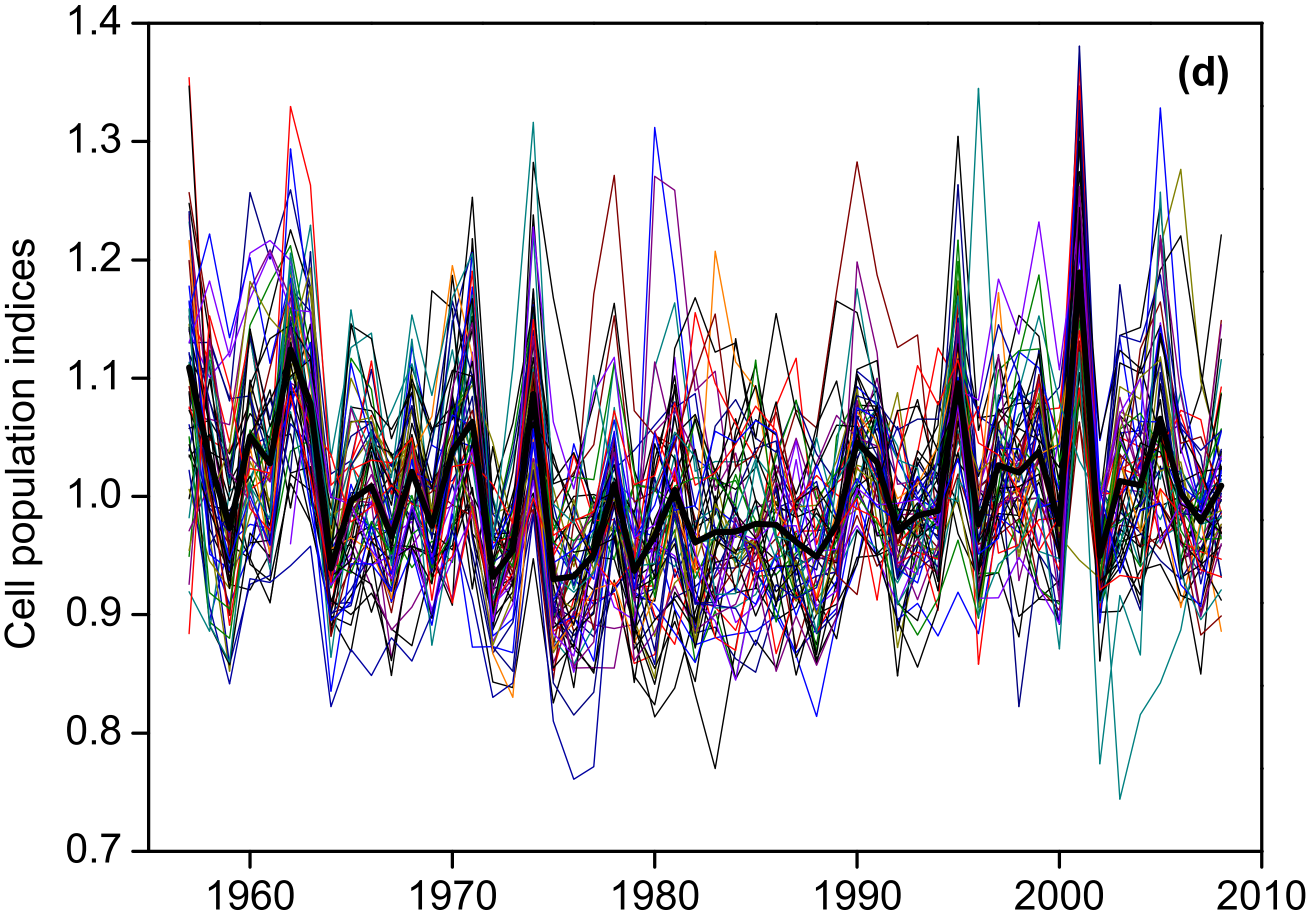

(d)
Cell population indices
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
1960
1970
1980
1990
2000
2010

Fig.3e

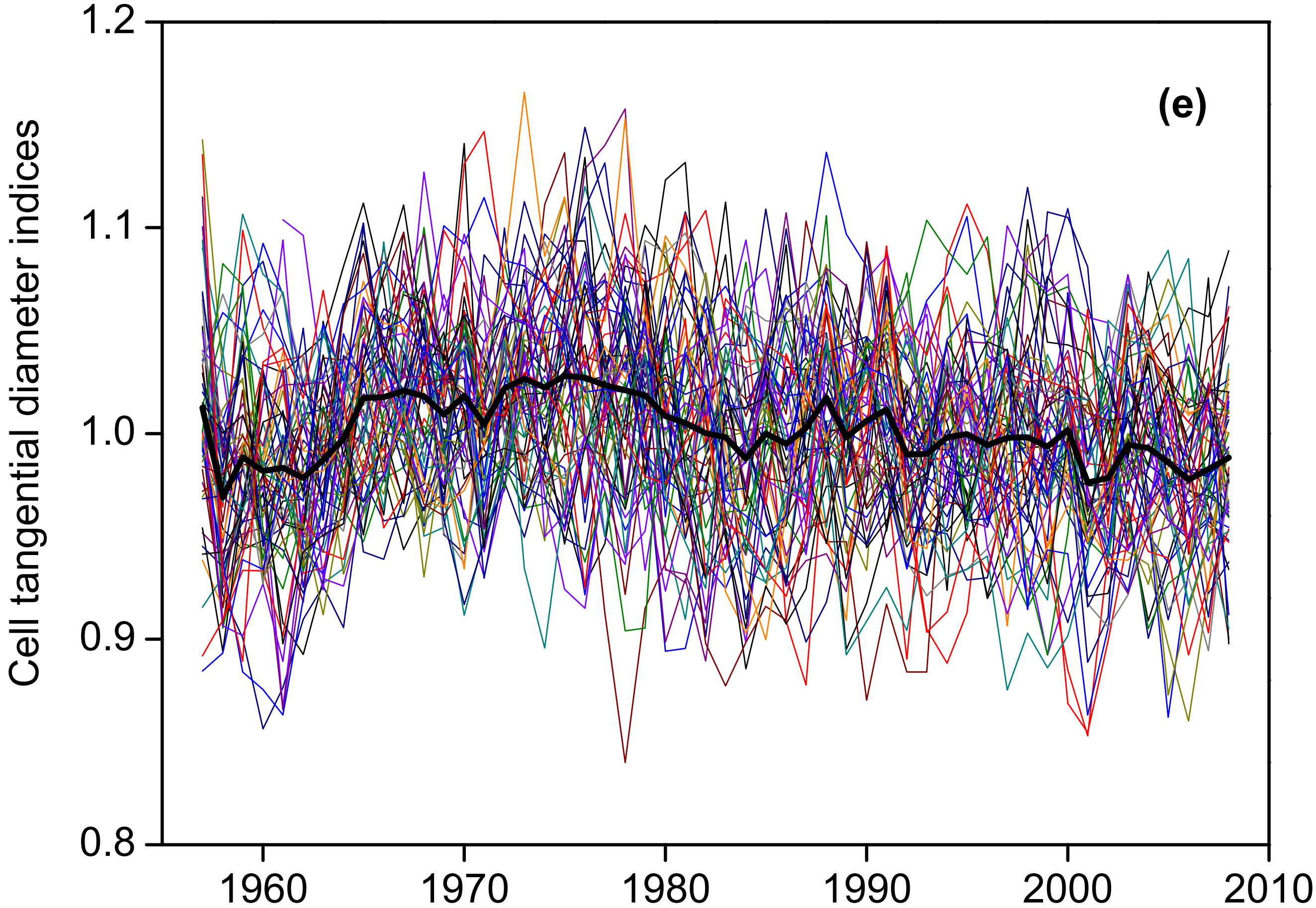
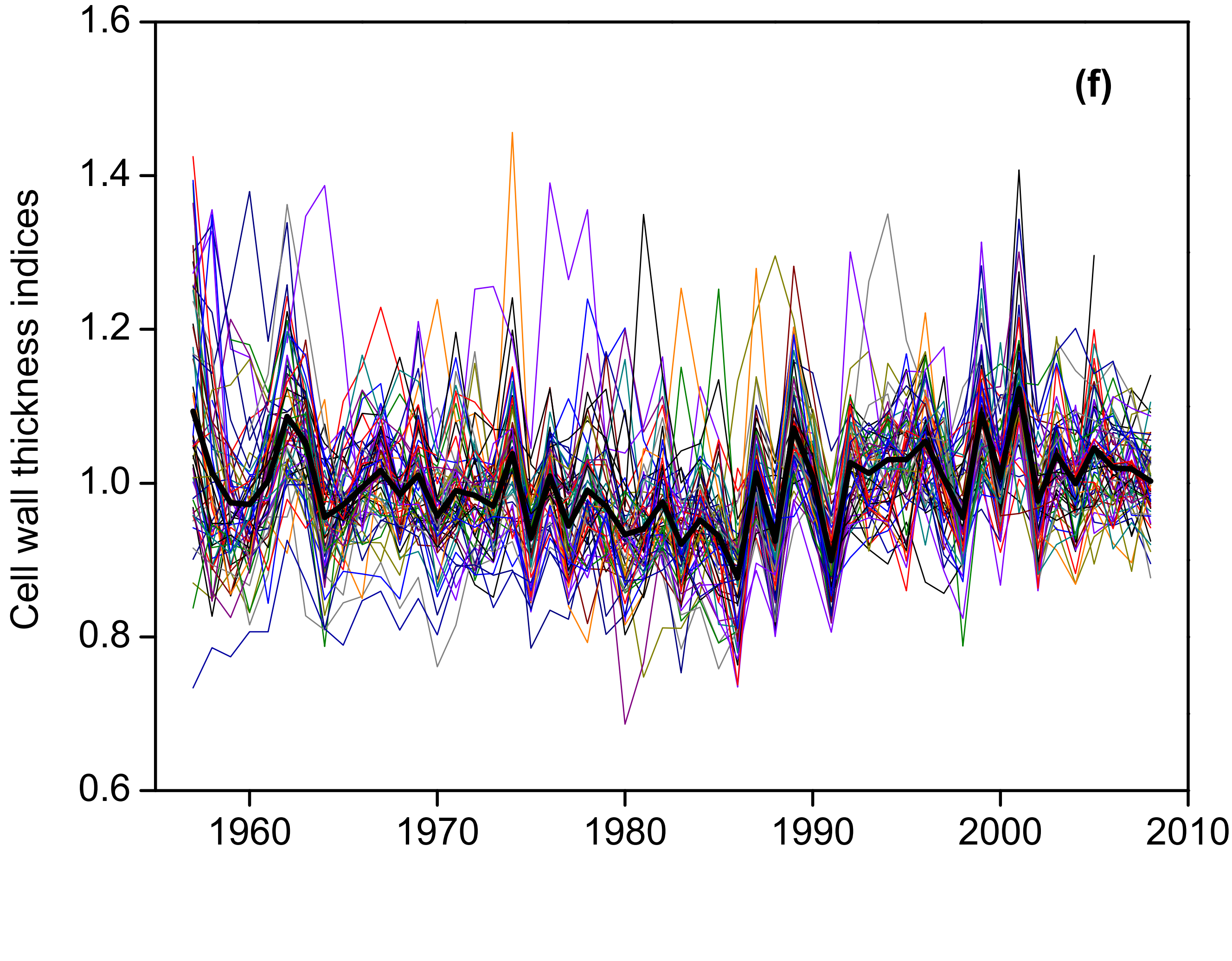
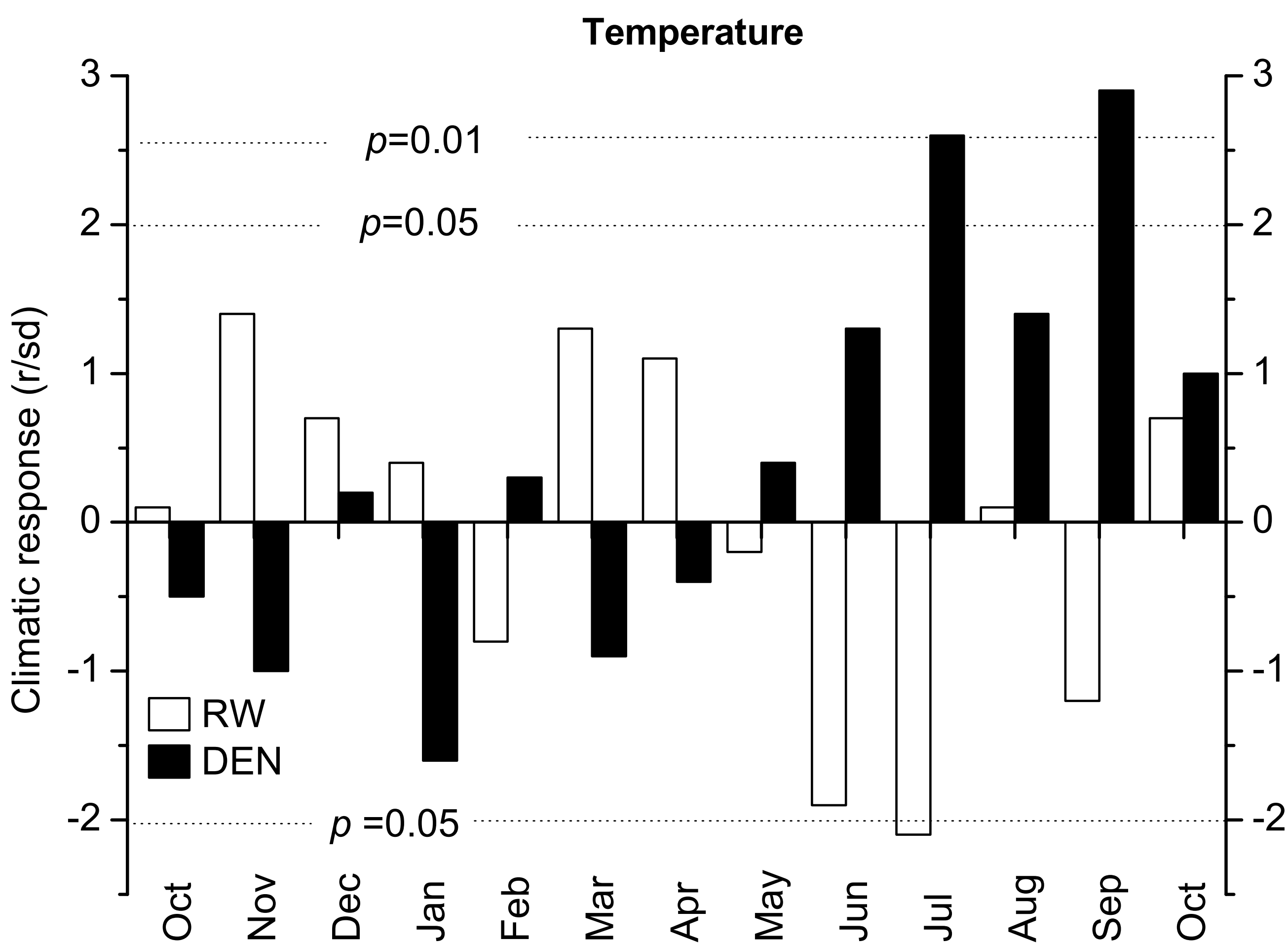

(e)
Cell tangential diameter indices
1.2
1.1
1.0
0.9
0.8
1960
1970
1980
1990
2000
2010

Fig.3f



(f)
Cell wall thickness indices
1.6
1.4
1.2
1.0
0.8
0.6
1960
1970
1980
1990
2000
2010

Fig.4



Temperature
3
2
1
0
-1
-2
p=0.01
p=0.05
p =0.05
Climatic response (r/sd)
RW
DEN
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct

Fig.4

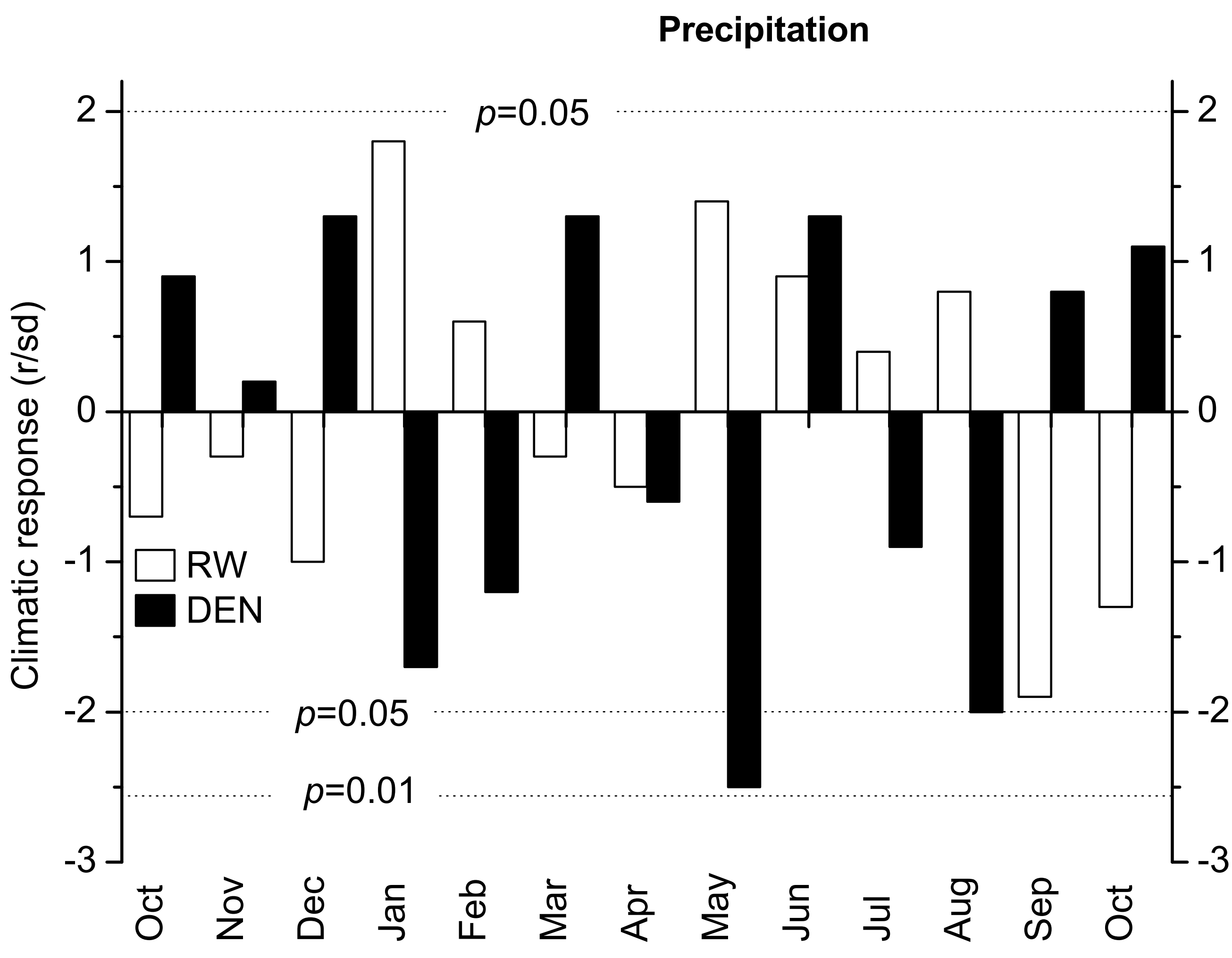

Precipitation
Climatic response (r/sd)
2
1
0
-1
-2
-3
p=0.05
p=0.05
p=0.01
RW
DEN
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct

Fig.4

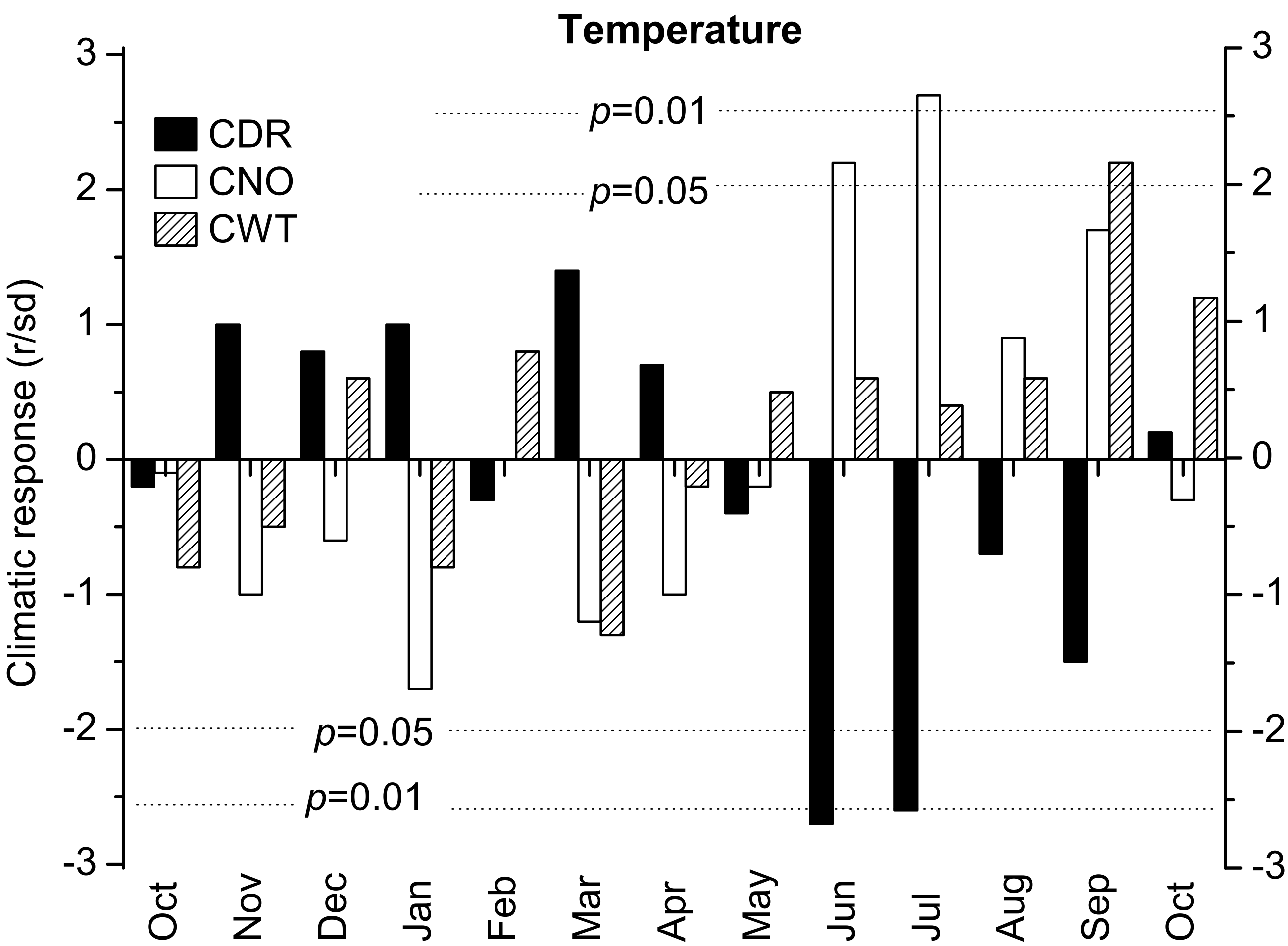
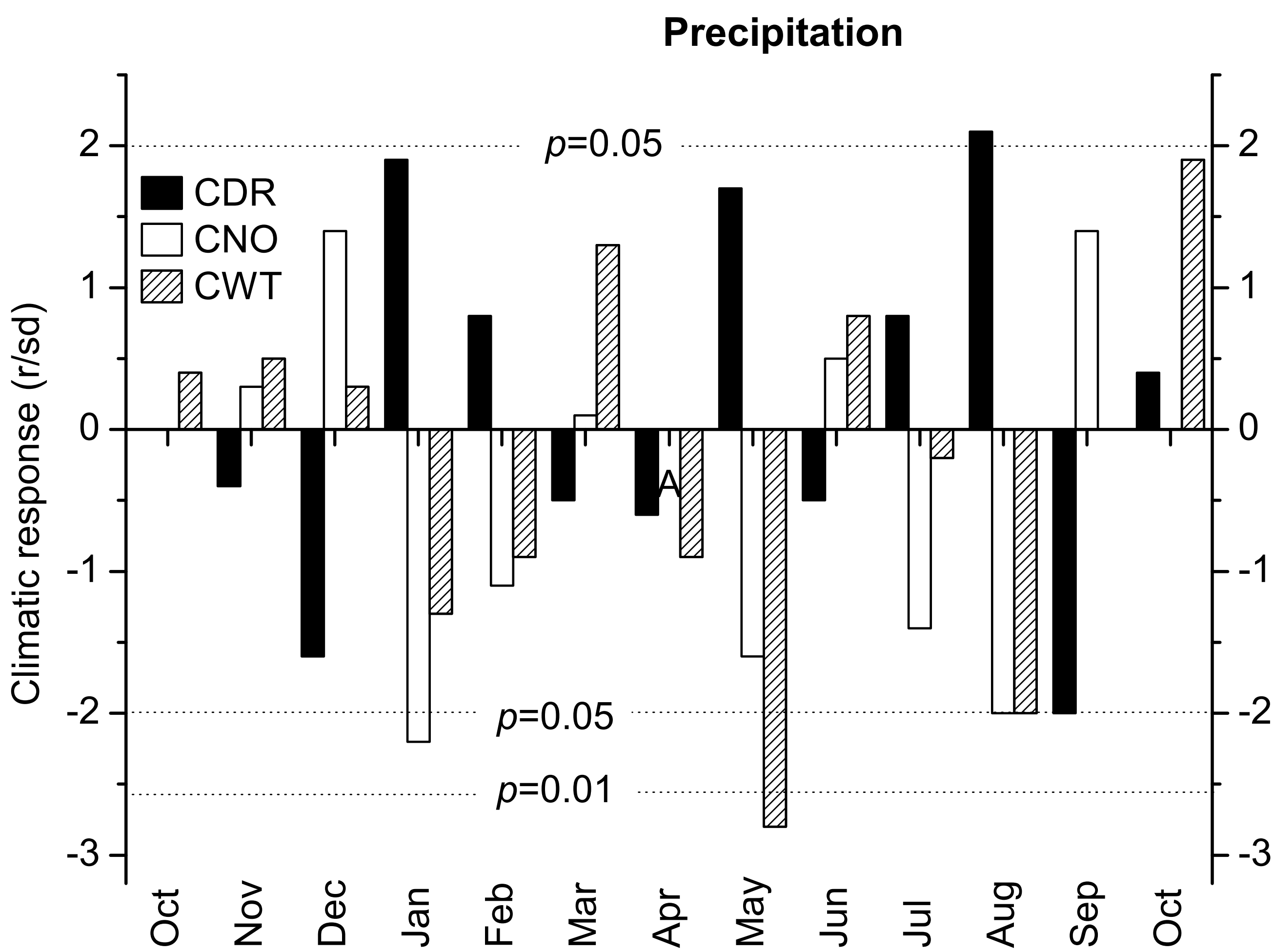

Temperature
CDR
CNO
CWT
p=0.01
p=0.05
p=0.05
p=0.01
Climatic response (r/sd)
3
2
1
0
-1
-2
-3
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct

Fig.4


Precipitation
p=0.05
CDR
CNO
CWT
p=0.05
p=0.01
A
Climatic response (r/sd)
2
1
0
-1
-2
-3
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct