

# Growth rate rather than growing season length determines wood biomass in dry environments

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## ABSTRACT

A number of studies have suggested that growing season length determines carbon sequestration of forest ecosystems. Given the possibility that drought-induced growth decline will be caused by a prolonged growing season under a warming climate, we investigated the effect of growth rate and duration of xylem production on annual wood biomass in drought-prone environments. We analyzed the intra-annual dynamics of wood formation in Qilian junipers (*Juniperus przewalskii*) from the semi-arid north-eastern Tibetan Plateau, China (2009–2014) and in ponderosa pine (*Pinus ponderosa*) from the hyperarid Mojave Desert in Nevada, USA (2015–2016). Most variability in the number of xylem cells ( $N_{\text{cell}}$ ) was related to growth rate ( $r_m$ ) rather than duration of cell production ( $D_{\text{cell}}$ ). At the Tibetan sites, 69.9% and 54.7% of variability in  $N_{\text{cell}}$  was attributable to  $r_m$  for the lower and upper treeline, respectively. Within the Mojave Desert site, 53.9% of the variability in  $N_{\text{cell}}$  was related to  $r_m$ . The growth rate in the Tibetan Plateau forest is affected by minimum temperature and precipitation. Thus,  $r_m$  is a primary control on wood biomass in conifer species of semi-arid forests. Under warmer and drier conditions, a longer growing season will not benefit xylem formation of conifers, and in turn warming-induced drought could limit carbon sequestration by reducing the rate of cell production.

## 1. Introduction

Forests assimilate around  $2.5 \times 10^{12}$  kg of carbon globally each year (Pan et al., 2011). The predominant contributor to such carbon sink is xylem formation, a primary biological process through which carbon dioxide is permanently and structurally fixed as wood in trees (Cuny et al., 2015). A positive relationship between net ecosystem productivity in forests and growing season length has been suggested by eddy covariance or remote sensing studies (Churkina et al., 2005; Griggs et al., 2003). The temperature-driven lengthening of the growing season associated to global warming is expected to increase forest productivity in temperate and boreal forests. However, forest declines following severe water deficit have been observed at sites characterized by a longer growing season (Barber et al., 2000; Chen et al., 2017; Dulamsuren et al., 2010; Hu et al., 2010; Liu et al., 2013; Peñuelas et al., 2011). Moreover, recent investigations conducted in arid environments of the Tibetan Plateau (Ren et al., 2015, 2018) and the

western US (Ziaco and Biondi, 2016; Ziaco et al., 2018) have highlighted the predominant role of water availability as a driver of xylogenesis onset and ending. These observations have challenged the general hypothesis that warming temperatures might lead to a longer growing season and increase wood biomass production, as summer drought stress might cause an earlier cessation of xylem formation (Gruber et al., 2010) and have multiple consequences for forest function (Meinzer et al., 2013).

Growth rate is an important factor involved in forest productivity. A similar amount of xylem cells can be produced either with a faster growth rate over a shorter growing season, or with a slower growth rate maintained for a longer period (Deslauriers and Morin, 2005; Ren et al., 2015). In conifer forests under cold climates, the rate of tracheid production mostly varies with temperature, and higher growth rates occur between June and July (Rossi et al., 2006c). In drought-prone areas, the rate of xylem production appears to be well adapted to changing moisture conditions, given that cambial division and xylem expansion

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are turgor-driven and depend on cellular water uptake and solute accumulation (Kozłowski and Pallardy, 2002). Under drought stress, growth rate can slow down or even approach zero (Fang and Zhang, 2018; Liang et al., 2016), counteracting or even exceeding the effects of the prolonged growing season on wood production. This results in abrupt growth decline, which can be observed as narrower or even locally absent growth rings (Liang et al., 2006, 2016; Rigling et al., 2002), and ultimately trigger abrupt growth decline. Therefore, we hypothesize that wood production under moisture-limited conditions is mainly determined by growth rate, rather than by growing season length.

During the past decade, eddy covariance has been widely used as a standard method for the estimation of seasonal fluctuations in carbon exchange between forest ecosystems and the atmosphere (Baldocchi, 2003). Its measurements provide a global view of carbon fluxes that includes different components, such as soil, wood, leaves, and fruits (Babst et al., 2014; Zweifel et al., 2010), and thus do not allow to disentangle the allocation of carbon to wood from that to other sinks. Furthermore, assessments using eddy covariance are usually not compatible with biometric assessments on inter-annual forest ecosystem carbon dynamics (Rocha et al., 2006; Zweifel et al., 2010). A detailed, process-oriented understanding of xylem formation is necessary to improve our knowledge of woody biomass production. *In situ* observations are also required to better identify the seasonal dynamics of wood formation, and to accurately quantify the contribution of rate and duration of growth on wood production.

The objective of this study was to accurately quantify the contribution of growth rate and growing season length on xylem biomass production. The number of xylogenesis studies conducted in naturally water-limited environments is still relatively scarce, likely for the remoteness of suitable areas and for the frequent irregular growth patterns exhibited by species exposed to periodical drought stress (Kane and Kolb, 2014). The Tibetan Plateau of central-east Asia, and the Mojave Desert of the southwestern US, share several climatic and environmental features, including a pronounced seasonality of precipitation, arid conditions in the spring, and the presence of an upper and a lower treeline (Hughes and Funkhouser, 2003; Liu et al., 2006; Zhang et al., 2015). These two regions are therefore ideal locations to investigate plant responses to drought, and particularly tree growth dynamics under episodic moisture supplies. Our main objective was to test the hypothesis that growth rate rather than the duration of wood formation determines wood biomass in drought-prone environments. We investigated seasonal dynamics of xylem growth and woody biomass production based on weekly observations of xylogenesis at the upper and lower treelines (3850 m and 4210 m a.s.l.) of a semi-arid forest of Qilian juniper (*Juniperus przewalskii* Kom.) on the northeastern Tibetan Plateau. We also utilized available xylogenesis data from a montane hyperarid stand of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) located in the Mojave Desert in North America.

## 2. Material and methods

### 2.1. Study site and sampling design

Two sites were selected in a semi-arid forest of Qilian juniper (*Juniperus przewalskii*) close to Dulan County on the northeastern Tibetan Plateau (36°00'N, 98°11'E) (Fig. 1). The sites are located at 3850 and 4210 m a.s.l. on slopes of average 15° steepness. In this area, Qilian junipers are ca. 500 years old. Five dominant and healthy trees were selected at each site for a total of 10 trees. Diameter at breast height was  $54 \pm 7$  and  $53 \pm 4$  cm at the lower and upper sites, respectively, and with an average height of 8 m. Wood formation was monitored for 6 years (2009–2014) (Ren et al., 2018). A hyperarid montane stand of ponderosa pine (*Pinus ponderosa*) located on a gentle west-facing slope within the Mojave Desert (36.59°N, 115.21°W, 2320 m a.s.l.) in southern Nevada (USA) was also selected (Fig. 1).

Twelve dominant or codominant ponderosa pines were selected for monitoring of wood formation over 2 years (2015–2016) (Ziaco et al., 2018). Diameter at breast height ranged from 32 to 76 cm, whereas tree height was between 8.1 and 13.4 m. The average age of the sampled trees exceeded 250 years.

Microcores were extracted weekly for Qilian juniper and biweekly for ponderosa pine from the stems at a height of around 1.3 m using a Trephor (Rossi et al., 2006a) and stored in a formalin-ethanol-acetic acid (FAA) solution and a 50% alcohol-water solution, respectively. The microcores were cut in transverse sections (9–12  $\mu$ m in thickness) using a rotary microtome, and then stained with a mixture of safranin, astra blue and ethanol (Ren et al., 2015), or a 0.15% aqueous solution of cresyl violet acetate (Ziaco et al., 2018).

### 2.2. Air temperature and precipitation

At the Tibetan sites, meteorological data were recorded from October 2012 by automated weather stations at the upper and lower treelines of Qilian juniper. Air temperature and precipitation were measured every 30 min and stored in data loggers. Minimum, mean, and maximum daily temperatures and daily precipitation were used for subsequent analyses. Data for the period between January 2009 to September 2012 were estimated using the measurements collected from a meteorological station in Dulan (36°18'N, 98°06'E; 3190 m a.s.l.), 32 km from the study sites. Average air temperature between 2009 and 2014 was  $-1.49$  and  $0.04$  °C at the upper and lower treeline sites, respectively. Total annual precipitation was 433 and 364 mm at the upper and lower treeline sites, respectively, with approximately 1/2 of total annual precipitation falling in June–July (Ren et al., 2018).

At the ponderosa pine site, data from the meteorological station between 2011 and 2016 showed that average air temperature was  $10.2$  °C and total annual precipitation was 338 mm, with approximately 1/3 of total annual precipitation falling in July–August (Ziaco et al., 2018).

### 2.3. Wood production data

Sections were examined under the microscope at  $100\times$  magnification to observe cells in different stages of xylem differentiation. Cells in enlargement, secondary wall thickening and mature phases were counted along three radial rows. In spring, xylogenesis was considered to have started when at least one radial file of enlarging cells was observed (Rossi et al., 2006b). When no new enlarging cells were observed, wood production was considered to be finished. Given that woody biomass production was mostly calculated by cell wall thickness and that the amount of wall material per cell was quite constant along the rings (Cuny et al., 2015), the number of xylem cells in a ring was used to evaluate woody biomass production. The results of 2013 at Qilian juniper sites were not used because spring and autumn samples were not available.

### 2.4. Data analyses

Data from Dulan and the Mojave Desert were used to quantify the contribution of growth rate and the duration of wood formation to xylem growth (i.e. number of tracheids in fully formed xylem growth ring). Gompertz functions (NLIN procedure in SAS) were applied to compute the rate of xylem cell production ( $r_m$ ) (Rossi et al., 2003). The duration of the growing season is represented by the period of xylem cell production ( $D_{cell}$ ), between the beginning and cessation of cell enlargement.  $N_{cell}$ , defined as the median radial number of tracheids observed at the end of the growing season, was modeled by multiple regressions as a function of  $r_m$  and  $D_{cell}$  (Rathgeber et al., 2011). A sensitivity analysis of the model was performed to determine the specific contribution of growth rate and duration on wood production. This analysis consisted in computing the impact of relative variation of the

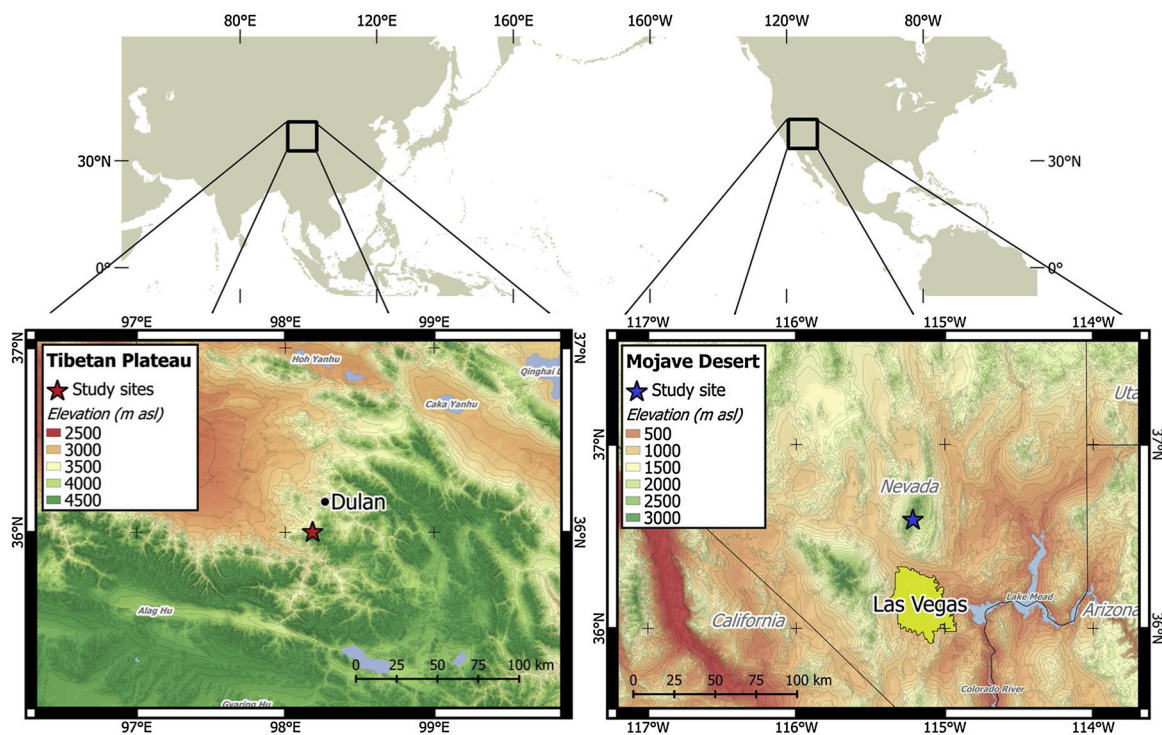


Fig. 1. Geographical location of the study sites in the Tibetan Plateau and in the Mojave Desert.

input variables, according to their standard deviations, on the results of the model.

The relationships between amount and timings of wood formation and climatic factors in Dulan were assessed with linear mixed models using site as a co-variable (Mixed procedure in SAS). In the model, tree was considered as a random factor. Climate included the average minimum ( $T_{min}$ ), mean ( $T_{mean}$ ) and maximum temperatures ( $T_{max}$ ) and sum of precipitation ( $PPT$ ) from June to July, the main period when xylem production occurs at the Tibetan sites (Ren et al., 2015). The linearity of the relationships and model fit were verified with the Studentized residuals (Quinn and Keough, 2002).

### 3. Results

#### 3.1. Characteristics of wood production

At the lower treeline of Qilian juniper, the average number of xylem cells along the radial files was 16.4, with the lowest number recorded in 2011 (Fig. 2). The duration of cell production varied between 46 and 71 days, with the longest duration recorded in 2012. Overall, the rate of cell production was 0.17 cells day<sup>-1</sup>, with the lowest rate in 2011. The year 2010 was characterized by the highest production rate and the shortest duration.

At the upper treeline of Qilian juniper, an average of 19.9 cells was produced, with the lowest number of cells in 2014 (Fig. 2). Cell production lasted between 42 and 71 days, with the shortest duration in 2014. The rate of cell production ranged between 0.18 to 0.25 cells day<sup>-1</sup>. The year 2010 was characterized by the highest cell production, corresponding to both the highest production rate and the longest duration.

#### 3.2. Rate vs. duration of wood production

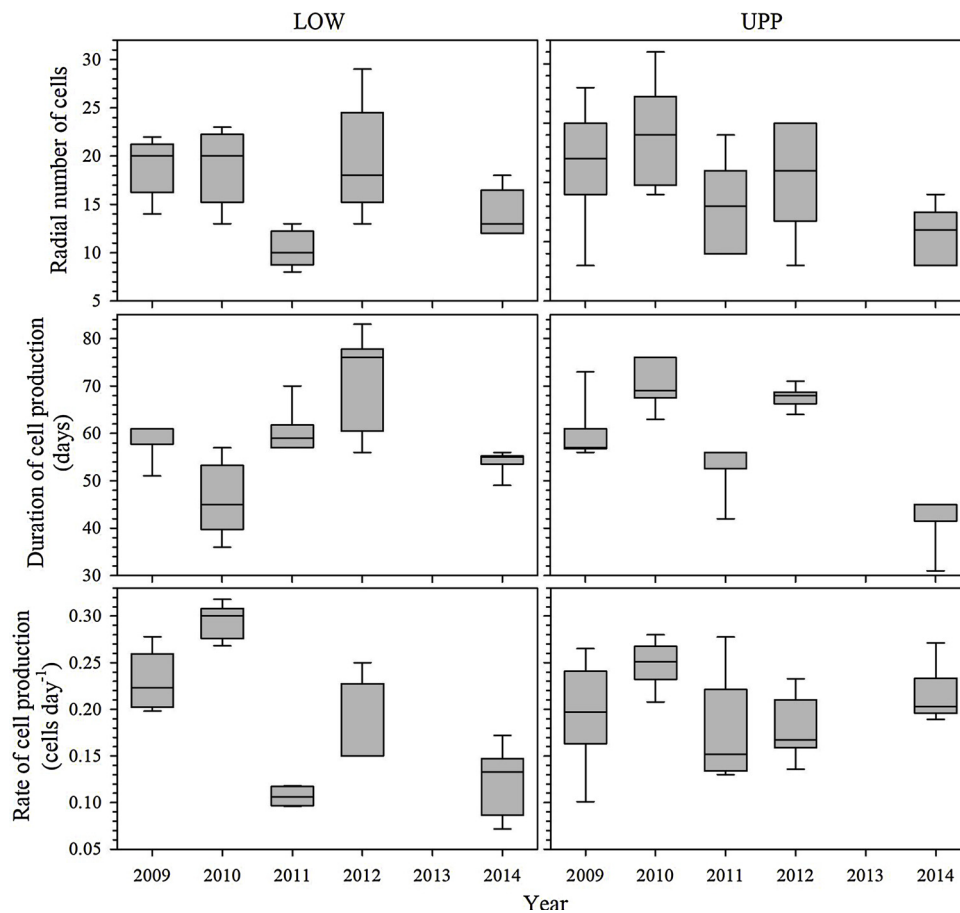
The model relating  $N_{cell}$  with  $D_{cell} \times r_m$  produced satisfactory estimates, with  $R^2$  of 0.66 ( $F = 44.39$ ,  $P < 0.01$ ) and 0.63 ( $F = 38.56$ ,  $P < 0.01$ ) at the lower and upper treelines of Qilian juniper, respectively (Fig. 3). At the lower treeline, 30.1% of the variability in  $N_{cell}$  was

attributable to  $D_{cell}$ , while 69.9% was attributable to  $r_m$ . When  $r_m$  was kept constant to its mean value,  $N_{cell}$  only varied from 14.6 to 19.0 cells (i.e. a range of variation of 4.4 cells) with  $D_{cell}$  varying around its mean within a range of twice its standard deviation. With a mean value of  $D_{cell}$ ,  $N_{cell}$  varied from 11.7 to 21.9 cells (i.e. a range of variation of 10.2 cells) when  $r_m$  varied around its mean within a range of twice its standard deviation. At the upper treeline of Qilian juniper, 45.3 and 54.7% of the variability in  $N_{cell}$  were related to  $D_{cell}$  and  $r_m$ , respectively. When  $r_m$  was kept constant to its mean value and  $D_{cell}$  varied around its mean within a range of twice its standard deviation, the resulting  $N_{cell}$  varied from 17.5 to 22.3 cells (i.e. a range of variation of 4.8 cells). Similarly, when  $D_{cell}$  was kept constant to its mean, and  $r_m$  varied around its mean within a range of twice its standard deviation, the resulting  $N_{cell}$  varied from 17.0 to 22.8 cells (i.e. a range of variation of 5.8 cells).

Xylogenesis data for ponderosa pine from the Mojave Desert support our findings from the dry Qilian juniper forests. Within the Mojave Desert, 46.1 and 53.9% of the variability in  $N_{cell}$  were related to  $D_{cell}$  and  $r_m$ , respectively (Fig. 4). When  $r_m$  was kept constant to its mean value and  $D_{cell}$  varied around its mean within a range of twice its standard deviation, the resulting  $N_{cell}$  varied from 12.4 to 30.3 cells (i.e. a range of variation of 17.9 cells). Similarly, when  $D_{cell}$  kept constant to its mean value and  $r_m$  was varied around its mean within a range of twice its standard deviation, the resulting  $N_{cell}$  varied from 8.4 to 34.3 cells (i.e. a range of variation of 25.9 cells).

#### 3.3. Wood production vs. climatic variables

$D_{cell}$  at the upper treeline of Qilian juniper gradually increased with precipitation (Fig. 5h). A similar pattern was observed for  $r_m$  at lower treeline, with higher  $r_m$  values observed in wetter years (Fig. 5l). Moreover,  $r_m$  at both lower and upper treelines of Qilian juniper gradually increased with increasing minimum temperature (Fig. 5i). Such relationships were well represented by the regression models, and further confirmed by the subsequent diagnostic tests (Fig. S1, Table S1).  $R^2$  represented satisfying values between 0.52 and 0.80. The Studentized residuals showed scatter of homoscedastic points and with a



**Fig. 2.** Radial number of xylem cells, duration of xylem production and rate of xylem production in *Juniperus przewalskii* recorded in 2009–2014 at the lower (LOW) and upper (UPP) treelines. Boxes represent upper and lower quartiles, whiskers achieve the 10th and 90th percentiles, and the median is drawn as horizontal solid line.

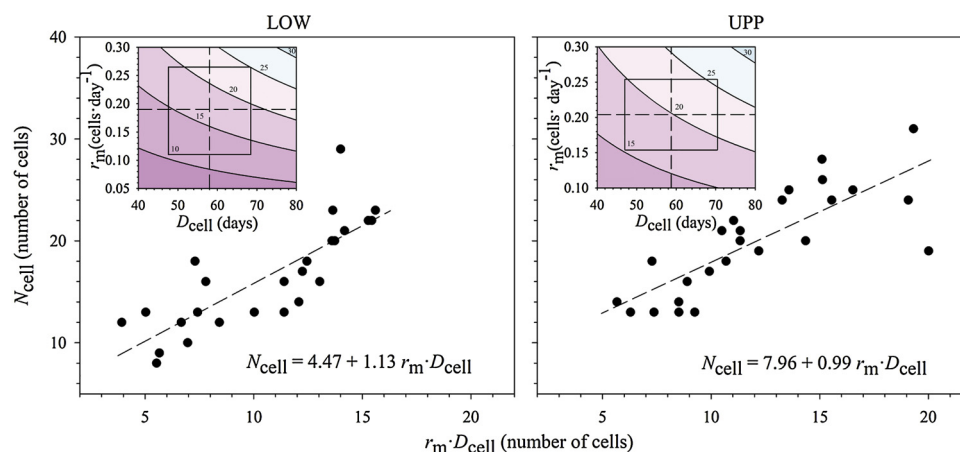
normal distribution of errors. Occasionally, pattern slightly diverging by the linearity were observed, which were detected by low  $R^2$ .

Minimum temperature (Model I) and precipitation (Model IV) showed significant impacts on wood production, defined as number of cells (Table 1). For  $N_{\text{cell}}$ , the effects of the minimum temperature were significant ( $P < 0.05$ ), while site and the interaction between the minimum temperature and site had no significant influence. For  $D_{\text{cell}}$ , the interaction between the minimum temperature and site, and the site showed significant effects, but not the minimum temperature. In addition, both site and minimum temperature, as well as their interaction, affected the rate of cell production. A similar pattern, but stronger and more significant, was observed for precipitation (Table 1). Precipitation

alone was the main determinant of the rate of cell production  $r_m$ , and to a minor extent the number of cells. The effect of site and its interaction with precipitation was instead predominant for the duration of cell production  $D_{\text{cell}}$ . The effects of mean temperature were reflected on  $r_m$  (Model II). No significant effects of site, maximum temperature, and their interaction (Model III) on wood formation were found.

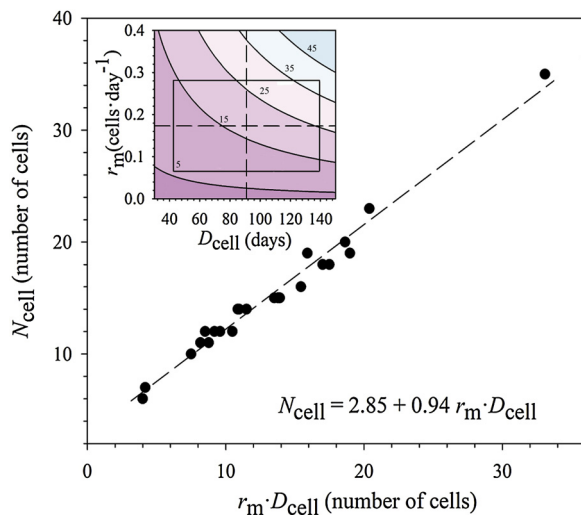
#### 4. Discussion

In the annual cycle of tree growth and dormancy, wood biomass production is controlled by both xylem production rate and growing season length. The seasonal dynamics of xylem formation is



**Fig. 3.** The simple physical model of the total number of xylem cells ( $N_{\text{cell}}$ ), the period of xylem cell production ( $D_{\text{cell}}$ ) and the xylem growth rate ( $r_m$ ) in *Juniperus przewalskii* as well as the sensitivity analysis of the physical model at the lower (LOW) and upper (UPP) treelines.





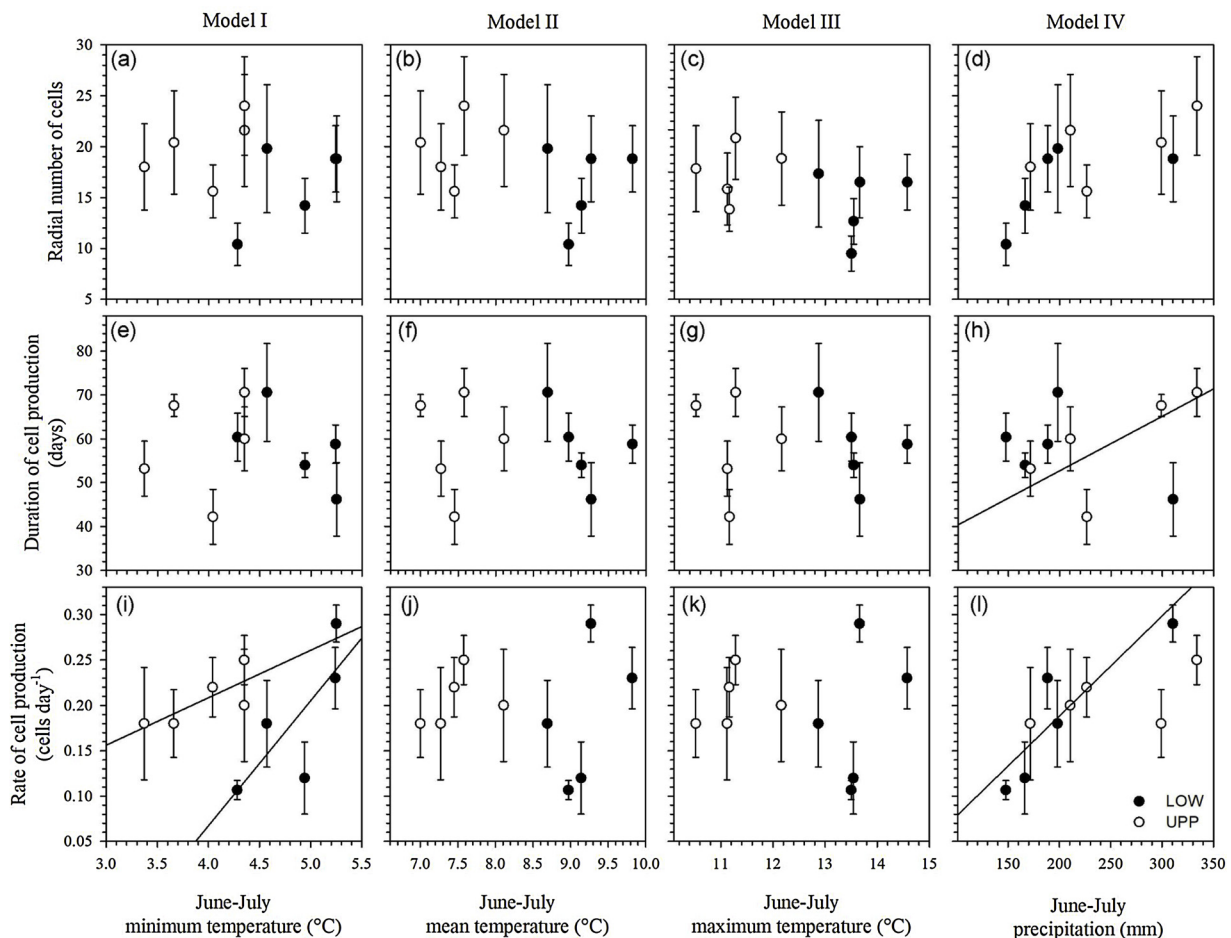
**Fig. 4.** The simple physical model of the total number of xylem cells ( $N_{\text{cell}}$ ), the period of xylem cell production ( $D_{\text{cell}}$ ) and the xylem growth rate ( $r_m$ ) in *Pinus ponderosa* as well as the sensitivity analysis of the physical model at the Las Vegas.

characterized by a S-shaped curve (Rossi et al., 2003), while the growth rate is described by a bell-shaped curve. It has been long assumed that wood biomass production is positively related to the growing season

length (Churkina et al., 2005; Griffis et al., 2003). In this study, however, the sensitivity analysis of our model shows that most variability in xylem formation at the two drought-prone regions, particularly in the amount of wood formed annually, can be better explained by the growth rate. Due to the calculation method, the rate of wood cell division is not a parameter perfectly independent from the total number of cells. However, based on the previous literature (e.g. Rathgeber et al., 2011; Rossi et al., 2014; Zhang et al., 2018) the results are reliable and can be representative of the observed trend in xylem growth. The rate of cell production was in fact the dominant factor in controlling xylem growth in Qilian juniper at the lower and upper treelines on the Tibetan Plateau and in ponderosa pine in the Mojave Desert. Zhang et al. (2018) found that the number of xylem cells in *Juniperus przewalskii* is substantially more sensitive to the growth rate but only marginally sensitive to the duration of cell production. Moreover, with an extremely dry and hot July, only 25% radial growth variability in *Abies alba* was attributable to the duration of cell production and 75% to its rate (Rathgeber et al., 2011). These findings suggest that wood production in drought-prone environments is determined by the growth rate rather than the length of the growing season, and that this pattern is consistent in semi- to hyper-arid regions of the globe, which allowed to accept our initial hypothesis.

#### 4.1. The determinant of wood production

The determinant of wood production varied with changing environmental conditions. The seasonal cambial cell production is highly



**Fig. 5.** Radial number of cells, duration of cell production and rate of cell production in *Juniperus przewalskii* vs. the June-July temperatures and precipitation recorded in the study years at the lower (filled dots) and upper (open dots) treelines. Dots represent means and error bars indicate the standard deviation. Solid lines represent significant ( $P < 0.05$ ) linear regression.

**Table 1**

Statistical parameters ( $F$ , significance level  $P$ ) of linear mixed models based on radial number of cells, duration of cell production and rate of cell production in *Juniperus przewalskii*.

	Model I			Model II			Model III			Model IV		
	Site	$T_{min}$	$S \times T_{min}$	Site	$T_{mean}$	$S \times T_{mean}$	Site	$T_{max}$	$S \times T_{max}$	Site	$PPT$	$S \times PPT$
Radial number of cells ( $N_{cell}$ )	1.09	7.58*	0.30	0.01	1.44	0.02	0.03	0.48	0.11	0.44	9.35**	0.10
Duration of cell production ( $D_{cell}$ )	6.35*	0.92	6.10*	1.47	1.72	1.20	0.70	1.95	0.51	19.66**	0.88	20.77**
Rate of cell production ( $r_m$ )	9.02**	25.32**	5.85**	2.48	5.08*	1.71	1.37	2.35	0.97	11.84**	38.67**	14.80**

$T_{min}$ , June–July minimum temperature;  $T_{mean}$ , June–July mean temperature;  $T_{max}$ , June–July maximum temperature;  $PPT$ , June–July precipitation.

One and two asterisks indicated  $P < 0.05$  and  $P < 0.01$ , respectively.

variable and plastic, depending on temperature and precipitation (Gricar et al., 2014). In our study sites, the duration of cell production had a limited impact on final number of tracheids. Despite of suitable thermal conditions, xylogenesis in semi-arid forests occurs when specific moisture conditions are satisfied. The onset of xylogenesis in *Juniperus przewalskii* occurs when cumulative precipitation within 12 days is more than  $17.0 \pm 5.6$  mm (Ren et al., 2018). Ziaco et al. (2018) found that the formation of new xylem cell layers in ponderosa pine shifted by more than two months in the Mojave Desert site included in this study depending on moisture conditions, and in particular on the balance between cold-season vs. monsoonal precipitation. The negative impacts of drought on growth rate can exceed the potential beneficial effects of a temperature-driven extension of the growing season. Several studies have found that growth rate decrease sharply with drought, tending to zero in the most extreme cases. For example, the average growth rate in *Abies pinsapo* decreased from 2.17 to 1.27 tracheids  $\text{day}^{-1}$  under drought stress (Linares et al., 2009). Similarly, after a water-deficit period, the number of cambial cells significantly decreased in *Picea mariana* saplings (Balducci et al., 2013). In addition, cambium in *Picea mariana* stopped with divisional activity under severe water deficit (Deslauriers et al., 2016). The cessation of cellular division shortens the actual growth period, contributing significantly to the variation in annual wood biomass. Extremely low growth rates might also explain the frequency of locally absent tree-rings that is commonly observed in water-limited regions, particularly in the southwestern US (George et al., 2013). On the other hand, temporary improvements of moisture conditions may lead to a bimodal pattern of xylogenesis, as observed in Mediterranean regions characterized by spring and autumn precipitation (Camarero et al., 2010; Vieira et al., 2013).

In temperate and boreal forests with sufficient water supply, both duration and intensity of cell production play an important role in xylem formation. Xylogenesis in spring occurs when the specific critical temperatures are reached (Li et al., 2017; Rossi et al., 2008). Spring warming induces an earlier onset of xylogenesis, extending the growing season length, and therefore allowing more time for cambial cells to divide and produce new tracheids (Menzel and Fabian, 1999). The effect of temperature on growth rate has been confirmed in several studies. For example, Deslauriers and Morin (2005) showed that the rate of xylem production in *Abies balsamea* was largely dependent on minimum air and soil temperatures. The rate of xylem production in *Picea abies* was significantly correlated with daily mean temperature (Mäkinen et al., 2003). In addition, dominant trees tend to exhibit higher temperature sensitivity of tracheid production rate than suppressed trees (Liu et al., 2018). Therefore, higher temperatures tend to speed up cell production, leading to higher rates of cell division. However, Körner (2003) observed non-linear relationship between the rate of cell division and temperature; namely cell doubling time decreased exponentially when the temperature rose from 5 to 10 °C, but was quite constant at temperature of 10 to 25 °C. Thus, in temperate and boreal ecosystems with good moisture conditions, the impact of growth rate on total radial increment is generally less respect to the duration (Lupi et al., 2010). When growth rate is suppressed by warming-induced water deficits, the contribution of growth duration to wood production

decreases. As a result, no correlation between the growing season length and wood biomass has been observed (Dunn et al., 2007).

#### 4.2. Effects of climate on wood production

Climatic factors, such as temperature and precipitation, influence wood production by simultaneously affecting the rate and duration of cell production. For example, climate warming led to a longer growing season, but reduced the growth rate due to decreasing snow melt water in spring, thus resulting in the declining trend of annual carbon uptake in the Colorado Rocky Mountains (Hu et al., 2010). Similarly, warming-induced earlier springs decreased summer peak growth rate in the North American boreal forests, which may have contributed to the declining trend of wood productivity associated with the climatic warming at high latitudes in the past few decades (Buermann et al., 2013). Meanwhile, the higher sensitivity to early- and mid-season droughts suggests that the timing of drought also has a decisive influence on the woody biomass productivity. A recent analysis in temperate mesic forests of Eastern North America showed that the impacts of drought on radial growth are most relevant when water deficits occur during peaks of xylem growth, and least crucial when droughts occur late in the growing season (D'Orangeville et al., 2018). This is probably because the cell production rate, which follows a positive exponential growing phase followed by a decline in growth rate, provides a greater contribution to xylem production.

#### 5. Conclusion

In conclusion, our study highlighted the quantitative relationship linking wood biomass with the rate and duration of xylem production under water-limited conditions. We showed that most variability of wood formation in drought-prone environments can be explained by the rate of xylem production rather than its duration. Our findings are useful for estimating forest productivity and its seasonal dynamics, as they suggest a mechanistic basis to understand the effect of climate change on forest health. The global terrestrial net primary productivity has increased in the period 1982–1999 (Nemani et al., 2003), but declined after 2000 due to large-scale drought (Zhao and Running, 2010). Terrestrial gross primary productivity is jointly controlled by plant phenology and growth capacity (Xia et al., 2015). The annual net ecosystem productivity only correlated poorly with the change in growing season length (Piao et al., 2007). According to our finding, the effects of low wood production rate caused by drought have exceeded the potential benefits on wood biomass of a prolonged growing season in conifer species, and hence reducing net carbon uptake in arid and semi-arid environments. Thus, we conclude that xylem growth rates will be a primary determinant of wood biomass accumulation in conifers under warming and drying scenarios. However, it would be cautious in extrapolating results of this study to all other arid and semi-arid environments, especially with respect to those drought-prone environments which are dominated by deciduous tree species.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2019.02.031>.

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