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A Global Analysis of Temperature Effects on *Populus* Plantation Production Potential

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Abstract

The genus *Populus* contains some of the most economically important tree species and hybrids in the world. We compared productivity of short and long-rotation poplar plantations using published data from 23 countries to determine if climate, particularly temperature, had any effect on the observed patterns of productivity. We discovered that climate factors (related to temperature) and clone origin (pure species or hybrids) slightly influenced productivity of long rotation forests more than short rotation plantations. While long rotation plantation productivity exhibited positive correlations with increasing temperature during winter and decreasing heat during summer, short rotation plantations showed weak positive relationship among productivity and increasing yearly temperature and the number of hot days. It was apparent that short rotation plantations productivity was less dependent on regional climatic variables or origin of clone. However, it appears that overall, regardless of the system, *Populus* species are generally adapted to a range of climatic conditions where they are planted.

Keywords

Poplar, *Populus* sp., Hybrids, Fast-Growing Plantations, Intensive Forestry, Short and Long Rotation Plantations, Stem Volume, Climate

1. Introduction

The genus *Populus* is one of the most economically important woody plant genera in many parts of the world. Providing approximately 20 million m^3 of wood and fiber annually, *Populus* spp. are desirable because of their fast growth and versatile use of the wood. In addition to the many products from the wood, *Populus* spp. also

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provide many important environmental functions such as the rehabilitation of degraded lands, protection of soils and water, conservation of biological diversity, providing shelter and shade, and sequestering carbon in temperate and subtropical regions of the world [1].

Populus is a genus native to the Northern hemisphere, most commonly growing in mixed forests in North America and Eurasia. Globally, most (91%) of poplars are found in natural forests [2], however, planted forests represent a small, but rapidly expanding component, of poplar forests. There are nearly 5 million ha of poplar plantations worldwide and another 1.5 million ha in agroforestry systems. Most of these plantations (73% of global total) are planted in China [1] and the most commonly planted poplars in the world are *Populus* × *euramericana* and *P. deltoides* cultivars.

In the United States, the first reported poplar artificial regeneration program began in 1893 when the Willamette Pulp and Paper Company planted 400 hectares of *P. trichocarpa* in the Oregon [3]. Additional plantations were soon established elsewhere in the region and due to the success of these initial plantings, the forest industry has looked to poplar production as one way to satisfy a continuously increasing demand for woody fiber.

Poplars are globally cultivated typically using two primary strategies: short rotation coppices (SRC) with very dense planting and short harvest rotation, 2 - 5 years, and long rotation plantations (LRP) with a wider initial spacing and longer rotation, generally 15 - 30 years. The main purpose of planting trees in SRC is generally production of biofuel wood or pulp, frequently used for pelleting or chopping, whereas in LRP production industrial roundwood is the main goal. Thus, those schemes are determined by the final products and cost-effectiveness [4]. Differences in sensitivity to biotic and abiotic stressors may also be a factor in making decisions on rotation length.

One of the most desirable characteristics of poplars is their fast growth. In the United States, individual studies indicate a wide range of production rates from 5.4 to 30 Mg/ha/yr and results are dependent on a number of factors [5]-[8]. In terms of biomass production, Holzmueller and Jose [9] reported these values were comparable to the production of annual grain-based crops such as maize (7 - 9.7 Mg/ha/yr) and sorghum (4.5 Mg/ha/yr) [10] [11]. Such fast growth, however, is linked to short life span, with some *Populus* species reaching maturity at the age of 40 - 50 years.

The other primary reason *Populus* is so desirable for plantation production is that it is a very adaptable tree genus. It includes many species and hybrids that are able to grow under various conditions and have a wide spectrum of adaptations to biotic and abiotic stressors [12]. For example, De Woody *et al*. [13] demonstrated that *Populus nigra* leaf size was reduced and branching architecture changed across a north-south gradient in Europe. Villar *et al*. [14] suggest that some poplar species have genetic and ecophysiological characteristics to cope with the ongoing climate change that may allow us to use them successfully in the future.

The huge diversity of species, clones and hybrids, and the easy ability for interspecies hybridization for some species may be of great significance for adaptations. It has been suggested that crosses between European, American and Asian poplars, some of which occur naturally, are more tolerant to biotic and abiotic stressors, have better growth and productivity, and competitive ability. In a study of poplar hybrids in the western United States Stettler *et al*. [15] attributed these characteristics primarily to heterosis effects. In another example, crosses between European and American poplars showed superior performance in germination, survival rate, and shoot growth under elevated temperature, suggesting they may be more beneficial than pure species for plantation purposes [16]. It is possible that further performance increases may be achieved through genetic engineering [17]-[22]. However, the easiness of spontaneous hybridization between introduced and wild relatives may pose risks to the genetic integrity of native species and should bring some caution before introduction [23].

While poplar species are planted across the globe, there has been little analysis to compare production rates among plantations in different regions. Given the range of temperature within which poplars are planted and the different types of plantings, the objective of this study was to analyze patterns in productivity across a temperature gradient of two different types of *Populus* plantings, short rotation coppices (SRC) and long rotation plantations (LRP) for both pure species and hybrids.

2. Materials and Methods

Approximately 50 papers from 23 countries (North America, Eurasia, Australia) with more than 500 records (for short and long rotation plantations) were analyzed. While the list was not exhaustive we included as many studies from different regions and from different countries as possible. Only papers with available data about diameter and stem height at a given age, clearly described *Populus* species used, and type of plantation, SRC or LRP, were included. When possible, data about DBH were taken, but in a few studies, especially related to 1 year old SRC, only data on diameter at ground level were available. Annual stem volume indexes (SVI) were calculated based on DBH, height and age of trees by the formula: SVI = $(\mathrm{DBH}^2 * \mathrm{height})/\mathrm{age}$. Correlation analysis was applied for estimation of productivity for pure species and hybrids in two different systems of planting, SRC and LRP. Comparisons in the differences between regression lines were determined with the use of *t*-criteria ($P < 0.01$) [24].

As data about temperature conditions were presented in a small amount of publications, we collected parameters by obtaining them from an open-source database (http://www.weatherbase.com). Parameters were chosen based on importance for plant vegetation as well as accessibility from base data for most localities. Those parameters were: average annual temperature, average annual high temperature, average annual low temperature, highest recorded annual temperature, lowest recorded annual temperature, average number of days above 32˚C, average number of days above 0˚C. If the place signed in paper was not present in the base data, closest geographical place were chosen. Pearson correlation tests were used to quantify relationships between stem volume indexes and temperature data, relationships were accepted statistically significant under the level of $P < 0.01$.

Data about local soil conditions were included in our database but unfortunately were not used for analysis due to difficulties related to the wide range of soil classification. Data about irrigation, fertilization, chemicals used, altitude, longitude and elevation were not available in most publications, and therefore weren't applicable for analysis either.

3. Results

Ten different *Populus* species and 21 hybrids were used for analysis (**Table 1**). Both *Populus* spp. and hybrids were planted in LRP and SRC. Most plantations were established using either 15 - 30 cm length dormant hardwood cuttings (SRC and LRP) or 1-year-old rooted cuttings (preferably LRP). Spacing generally ranged from 0.5 × 0.5 m to 1.5 × 1.5 m for SRC and 2 × 2 m to 6 × 6 m for LRP. Calculated by stem volume index the average annual productivity per tree was 0.074 m^3/yr for LRP and 0.005 m^3/yr for SRC.

Comparison of growth parameters (DBH and height) for species and hybrids demonstrated that in LRP, hybrids are generally more productive than pure species, and the linear slope coefficient for hybrids was more than two times greater than those for non-hybrid *Populus* species (**Figure 1**). Tree height and DBH differences between slopes of regression lines were highly significant ($t = 10.80$, $t = 11.24$, respectively, $P < 0.01$). For SRC, tree height and DBH differences for hybrid and non-hybrid poplars were smaller and didn't differ significantly ($t = 1.84$ for DBH, $t = 0.03$ for tree height, $P > 0.05$; **Figure 2**).

Results of statistical analysis for estimation of the effects of temperature parameters on poplar tree productivity did not show any strong correlations, but there were some significantly weak correlations (within $0.20 < r < 0.32$, $P < 0.01$) (**Table 2**). For LRP, wood productivity slowly increased with increasing lowest recorded annual temperature and the numbers of days above 0˚C per year and decreased with increasing number of hot days above 32˚C. For SRC both average annual high temperatures and the number of hot days above 32˚C have significant weak positive influence on SVI (**Table 2**).

4. Discussion

Hybrid poplars are typically selected for high productivity and it is not surprising that on average hybrid poplars outperformed pure species planted as LRP. We expected to see similar results in SRC, but this was not the case. However if you were to compare the size of the best hybrids to the best species in SRC, the hybrids showed better growth (**Figure 1** and **Figure 2**). Decreased mean size in the SRC hybrids could be the result of the testing of experimental hybrids that would not typically be planted on a wide spread basis.

The lack of a strong relationship between temperature parameters and poplar growth could be explained by several factors. The first could be that while data from over 23 countries were analyzed, most of these plantations were in temperate environments, and the range in temperature parameters used in the analysis was not wide enough. In addition, poplar species are adapted to a wide range of conditions and commonly have extensive ranges. For example, the range of *Populus deltoides* (eastern cottonwood) extends from the southernmost United States to northern Canada. Therefore, given the wide latitude in which poplar species are naturally found differences in temperature may not influence poplar growth in most instances.

Table 1. *Populus* species analyzed in current research (listed by countries).

Populus sp.	Plantation	Country	Source
P. deltoides, *P.* × *euroamericana*	LRP	Australia	[25]
P. balsamifera × *P. deltoides*, *P. balsamifera* × *P. maximowiczii*, *P. balsamifera* × *P. trichocarpa*, *P. deltoides* × *P.* × *petrowskyana*, *P.* × *euroamericana*, *P. maximowiczii* × *P. nigra*, *P. maximowiczii* × *P. trichocarpa*	LRP, SRC	Canada	[26]-[29]
P. deltoides, *P.* × *euroamericana* × *P. nigra*, *P.* × *interamericana*, *P. nigra* × *P. trichocarpa*, *P. tomentosa*, *P. tomentosa hybrids*	LRP, SRC	China	[30]-[33]
P. angulata, *P. deltoides*, *P. nigra*, *P.* × *euroamericana*, *P. maximowiczii* × *P. trichocarpa*	LRP, SRC	Czech Republic	[34] [35]
P. tremula, *P. tremula* × *P. tremuloides*	LRP	Finland	[36] [37]
P. × *euroamericana*, *P.* × *interamericana*	SRC	France	[38]
P. trichocarpa, *P* × *interamericana*, *P. maximowiczii* × *P. nigra*, *P. maximowiczii* × *P. trichocarpa*	SRC	Germany	[39]
P. × *euroamericana*	SRC	Greece	[40]
P. alba, *P. deltoides*, *P. alba* × *P. grandidentata*, *P. deltoides* × *P.* × *euroamericana*, *P.* × *interamericana*	LRP	Hungary	[41]-[43]
P. deltoides	LRP	India	[44]-[48]
P. deltoides	LRP	Iran	[49]
P. deltoides × *P.* × *euroamericana*, *P.* × *euroamericana*, *P.* × *generosa* × *P. nigra*	SRC	Italy	[50]
P. maximowiczii	SRC	Japan	[51]
P. × *euroamericana*	LRP	New Zealand	[52]
P. alba, *P. deltoides*, *P. nigra*, *P. trichocarpa*, *P.* × *euroamericana*, *P.* × *interamericana*	LRP, SRC	Romania	[53]
P. balsamifera, *P. tremula*, *P. tremuloides*, *P.* × *euroamericana*	LRP	Russia	[54]-[56]
P. deltoides, *P.deltoides* × *P.* × *euroamericana*, *P.* × *euroamericana*	LRP, SRC	Serbia	[57]-[59]
P. nigra, *P. angulata* × *P. nigra*, *P. deltoides*, *P.* × *euroamericana*, *P.* × *interamericana*, *P. maximowiczii* × *P. nigra*	LRP	Slovak Republic	[4] [60]
P. × *euroamericana*, *P.* × *interamericana*, *P.* × *interamericana* × *P. nigra*	SRC	Spain	[61]
P. balsamifera, *P. trichocarpa*, *P.* × *interamericana*, *P. maximowiszii* × *P. trichocarpa*, *P. deltoides* × *P. maximowiczii*, *P. tremula* × *P. tremuloides*	LRP	Sweden	[62] [63]
P. deltoides, *P. alba* × *P. deltoides*, *P.* × *euroamericana*	LRP	Turkey	[64] [65]
P. nigra, *P. balsamifera* × *P.trichocarpa*, *P.* × *euroamericana*, *P. laurifolia* × *P. nigra*	LRP, SRC	Ukraine	[66] [67]
P. deltoides, *P. nigra*, *P. trichocarpa*, *P. balsamifera x* (*P. laurifolia* × *P. nigra*), *P. deltoides* × *P. maximowiczii*, *P.* × *euroamericana*, *P.* × *interamericana*, *P. maximowiczii* × *P. nigra*, *P. nigra* × *P. trichocarpa*	LRP, SRC	USA	[68]-[73]

Table 2. Pearson's correlation coefficients relationships between yearly stem volume indexes (SVI) and temperature data.

Climate data	Range for long rotation plantations	Range for short rotation plantations	*r* (SVI), long rotation plantations	*r* (SVI). short rotation plantations
Average annual temperature	1.2 to 18.0˚C	1.2 to 15.1˚C	0.155*	0.109
Average annual high temperature	6.0 to 24.0˚C	7.0 to 20.3˚C	0.113	0.273*
Average annual low temperature	−4.7 to 13.0˚C	−4.7 to 11.0˚C	0.167*	−0.062
Highest recorded annual temperature	28.0 to 45.4˚C	33.0 to 43.2˚C	−0.060	−0.027
Lowest recorded annual temperature	−48.3 to −3.9˚C	−43.9 to −6.0˚C	0.206*	0.189
Average number of days above 32˚C per year	0 to 90	0 to 63	−0.228*	0.314*
Average number of days above 0˚C per year	158 to 362	158 to 343	0.300*	0.058

*correlation is significant under $P < 0.01$; weak correlations (within $0.20 < r < 0.32$) are underlined.

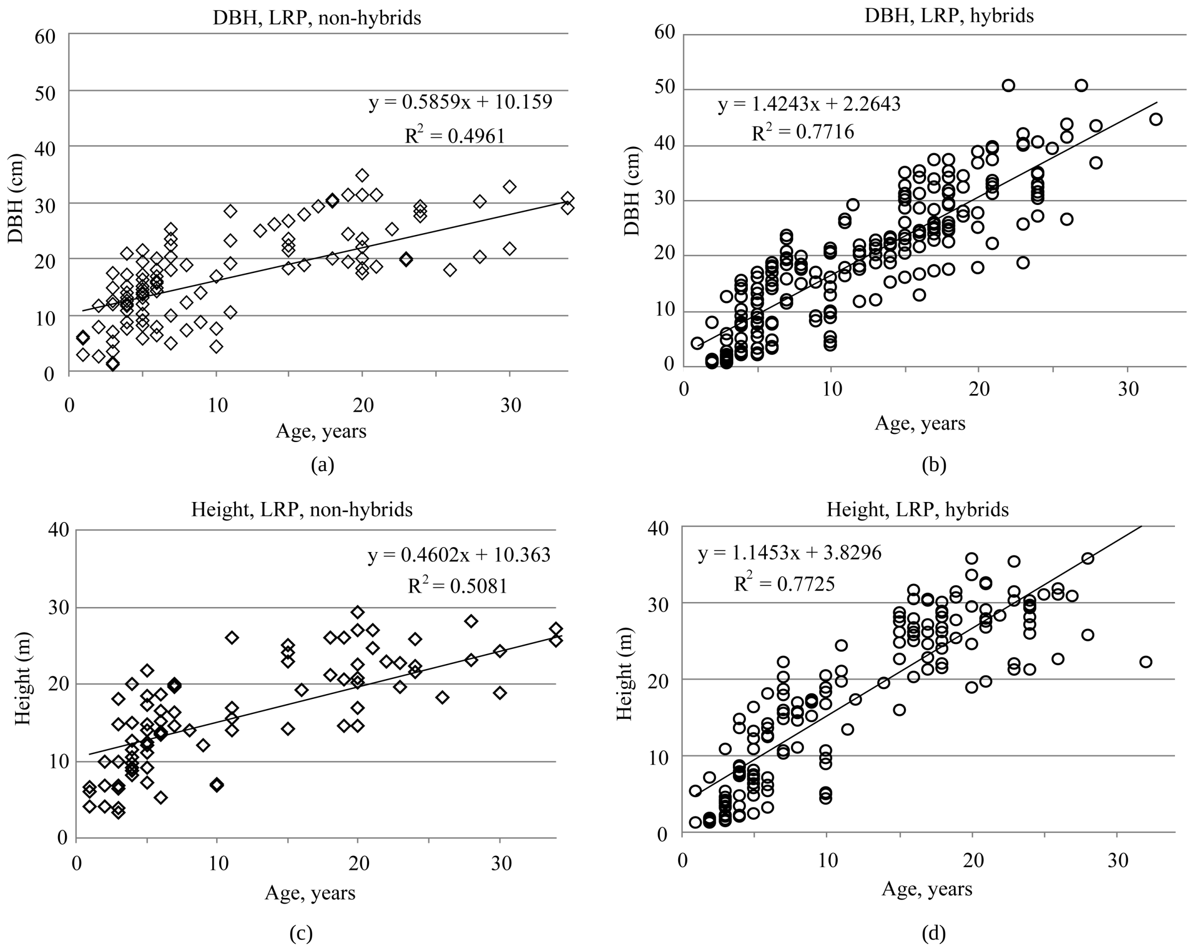

Figure 1. Age dynamics of DBH (a) (b) and height (c) (d) in long rotation plantations (LRP) for non-hybrid (a) (c) and hybrid (b) (d) poplar trees.

However, when analyzing productivity and temperature conditions, an interesting phenomenon was discovered. Indian plantations demonstrated sharp divergence from normal distributions and generally have higher productivity by stem volume indexes than plantations in other countries. We speculated that this effect was due to year-round favorable weather conditions as this was the only region that had zero days with temperature below 0˚C. Therefore, trees could grow without (or very short) dormant periods. From the first look it was unexpected as there was a weak negative relationship between poplar growth and number of hot days above 32˚C. But probably year-round favorable weather gives more benefits for poplar growth. Additional studies of poplars in warmer environments are needed to further test this hypothesis.

Other studies have suggested that water availability plays a larger role than temperature in poplar productivity [74]. Poplars are susceptible to drought and are commonly found in riparian regions, particularly in more arid environments. Jules *et al*. [75] observed that higher precipitation and cooler summers were positively correlated with plant growth. Conversely, some studies indicated that on a regional level, temperature can override the influence of precipitation levels. In a study of *Populus tremuloides* in British Columbia, positive correlations between tree height growth and mean annual temperature and mean annual summer temperature were observed, but no correlations were found for precipitation. Authors suggested that in this study growing season temperature was more limited than water availability [76].

In our study, LRP demonstrated some correlation between productivity and increasing temperature during winter and decreasing heat during summer; and for SRC, weak positive correlations between productivity and increasing yearly temperature and the number of hot days. Those findings may be partially based on the differences in range of parameters. While number of days above 32˚C for LRP ranged 0 to 90 days, for SRC it ranged

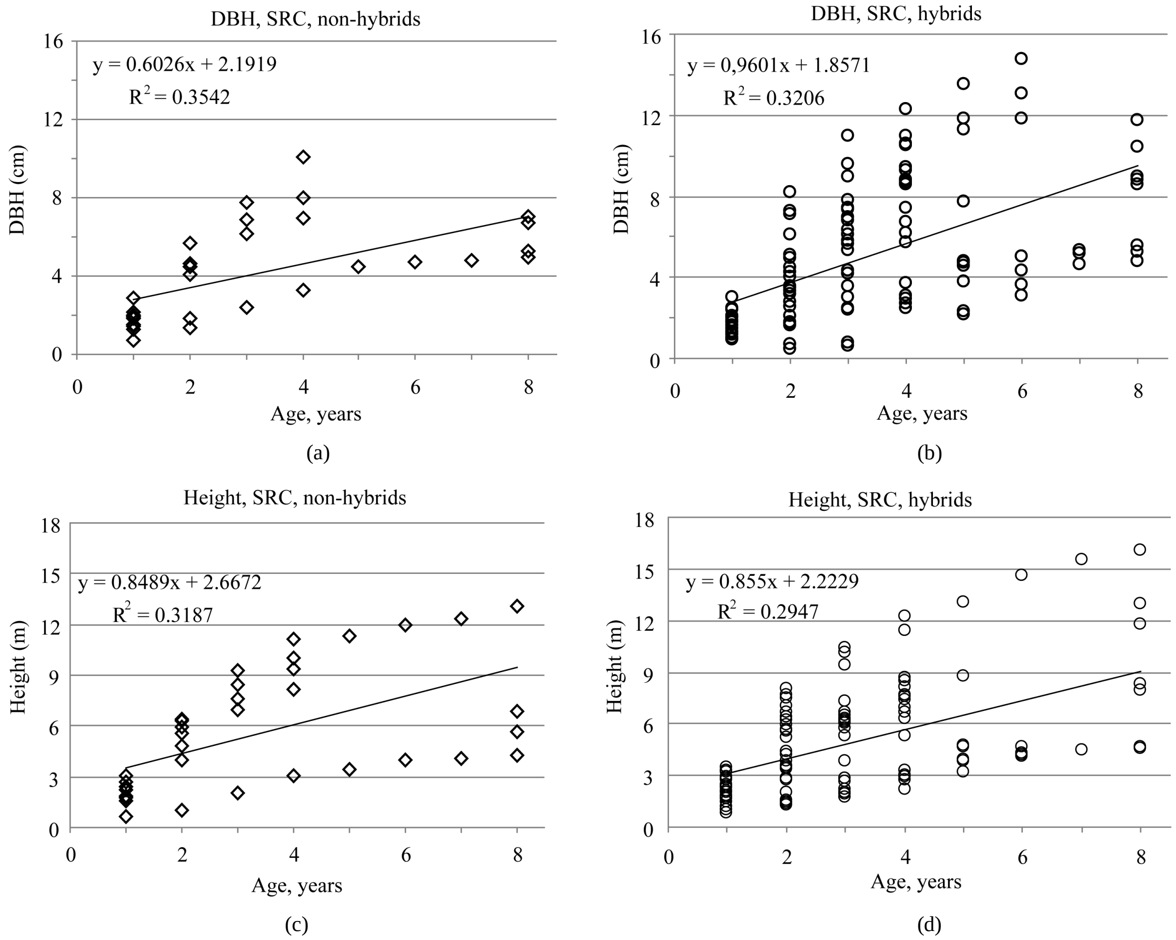

Figure 2. Age dynamics of DBH (a) (b) and height (c) (d) in short rotation coppices (SRC) for non-hybrid (a) (c) and hybrid (b) (d) poplar trees.

between 0 to 63 days (**Table 2**). We surmise that while too many hot days may be a limiting factor, it is probably reached after some critical threshold.

Climate parameters based on temperature, demonstrate that woody biomass production is possible under wide range of optimal temperature conditions. The number of hot summer days appears to decrease productivity in LRP; however, this may be offset by increased winter temperatures in these climates. High productivity for poplar plantations may be reached by using a broad genetic diversity of poplars and utilizing the highly adaptive potential of this genus. Overall, we observed an occurrence of a genotypic variability for productivity and some degree of sensitivity to environmental change in *Populus*, particularly for LRP. It is obvious that there is a wide range of adaptability for this genus, which is helpful to maintaining high levels of productivity even under predicted changes in future climate [75] [77]-[82].

5. Conclusion

We found that climate factors (related to temperature) and clone origin (pure species or hybrids) generally influenced production potential in long rotation plantations, but not in short rotation plantations. Opposite effects of number of hot days per year on LRP and SRC demonstrated that producing of wood in LRP was more vulnerable to the number of excessive heat days and an increase in number of excessive hot days. Our findings reveal that well managed SRC poplar plantations may have wider applications for regions with extreme temperature conditions, to which long rotation forests are more sensitive. It is most likely connected with more intensive early growth of poplar trees and may be offset with more active management of SRC, e.g. irrigation and fertilization. We conclude that SRC plantations appear to be less sensitive to environmental conditions than LRP irrespective of the geographic location. Overall, our analysis clearly indicates that growing *Populus* in SRC systems with proper cultural practices can decouple the effects of climate change on productivity.

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