Simulation of phytomass productivity based on the optimum temperature for plant growth in a cold climate

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Abstract It was found from more than 20-year lasting monitoring of the hydrologic cycle in 20 mountainous sites in the Czech Republic (altitude 600–1400 m a.s.l., vegetation season April–September: mean air temperature 8–10°C, mean precipitation total 400–700 mm, mean duration of sunshine 1100–1300 hours, and mean potential transpiration 200–250 mm) that plant temperature does not get over about 25 °C when plants transpire. According to the natural selection hypothesis, the phytocenosis able to survive the unfavourable conditions and produce the biggest amount of phytomass will be prevailing on the site occurring in the long-term stable natural conditions. Simulation of the phytomass productivity based on the optimum temperature for plant growth manifested that plants with the optimum temperature of about 25°C can survive the unfavourable conditions and produce the biggest amount of phytomass in the studied site in the long-term scale.

Key words: *phytomass productivity, plant temperature, plant transpiration, natural selection hypothesis, cold climate*

Introduction

The natural selection hypothesis (Eagleson, 1978) says that the plant cover will be prevailing on the site occurring in the long-term stable natural conditions that is able to survive the unfavourable conditions, and to produce the biggest amount of phytomass (similar to one of the strategies of maximal reproduction of the "selfish" gene by Dawkins (1989), as the second one includes production the biggest amount of diaspores). The second statement is based on the optimum temperature for plant growth defined as a temperature in which the plant growth (= production of phytomass) is maximal (Grace, 1988). It should be mentioned that there exists the plants with different optimum temperatures for their growth in the same habitat, and the same plant species could have different optimum temperatures according to the climatic conditions of its habitat (Larcher, 2003; Schulze et al., 2005).

Water exchange between the soil and plants is driven by heat from solar radiation that, in combination with the air temperature, is the cause of plant heating. The plants protect themselves by transpiration against heating up over the certain temperature (Larcher, 2003). In this way, heat input is divided into two parts – latent heat (used for water vaporization) and sensible heat. Sensible heat irradiated from plant cover is the dominant cause of heating of the low atmosphere layer. Water for transpiration is imbibed from the root zone of soil. In the case of water scarcity, transpiration ceases, the plants do not cool (the latent heat is equal to zero), and therefore, the plant cover and atmosphere are overheated by solar radiation. Simultaneously there are mineral nutrition and later on tree growth impaired (Grabařová, Martinková 2000, 2001). This relation between plant transpiration, soil water and income of solar energy is a core of co-evolution of plants, soil cover and climate (Kleidon, 2006).

The phenomenological theory of plant transpiration (Pražák et al., 1994) is based on the assumption that plant uses water vaporization for leaf cooling on the optimum temperature, and it brings good estimates of the daily sums of stand transpiration (Tesař et al., 2001). A close correlation of the daily stand transpiration to both the global radiation and air temperature was also presented by Střelcová et al. (2006), and it can be said that the transpiration is driven by heat input as it was presumed in the theory by Pražák et al. (1994).

The amount of water available for plant transpiration (mainly in the soil) and input of solar heat can form two markedly different states of things: (1) there is enough water for plant cooling by transpiration, and therefore, the plant transpiration is fully controlled by heat input in the hydrologic cycle (i.e. the heat-controlled hydrologic cycle), (2) the water source is insufficient, and therefore, the plant transpiration is limited by water scarcity in the hydrologic cycle (i.e. the water-controlled hydrologic cycle).

Since 1983, the hydrologic cycle has been monitored in 20 mountainous sites in the Czech Republic: Šumava, Krkonoše, Jizerské hory, Novobystřická pahorkatina. These sites lie in the altitude 600–1400 m a.s.l., in a cold climate region characterized in the vegetation season April–September by the mean air temperature 8–10ºC, mean precipitation total 400–700 mm, mean duration of sunshine 1100–1300 hours and mean potential transpiration 200–250 mm. They are covered with grass, dwarf pine forest and Norway spruce vegetation, and the soil is Cambisol, Gleyisol and Histosol (WRB, 1994). Geological bedrock, namely paragneiss or granite, forms an impermeable layer. In the climatic conditions of Czech mountains, the heat-controlled hydrologic cycle is predominating, and the water-controlled hydrologic cycle can be met once in seven years. On the basis of past climate reconstructions, it can be supposed that the heat-controlled hydrologic cycle has lasted permanently since the last glacial age, regardless of changing vegetation (Bodri & Čermák, 1997).

The monitored data describing the coupling between soil water tension (tensiometric pressure), transpiration, and temperature can be summarized as follows: (1) plant temperature does not get over the maximum temperature (about 25ºC) if there is enough water for plant transpiration, (2) in sunny days, scarcity of water for plant transpiration resulted in an increase in the plant temperature to about 35ºC and air temperature to about 30ºC, and (3) the limit value of tensiometric pressure, below which the water uptake for plant transpiration is impossible, was –60 kPa for grass, dwarf pine and Norway spruce stand in the course of vegetation season.

The aim of this study was to estimate the optimum temperature for plant growth in the studied area using the natural selection hypothesis and simulation of phytomass productivity.

Experimental area

Simulation of the phytomass productivity was done at the experimental area Zábrod – field (788 m a.s.l., Šumava Mts.) with permanent grass cover. Climatic characteristics of a typical growing season are presented in Table 1. The soil is an acid brown soil and three soil horizons 0–17 cm, 17–60 cm and 60–100 cm have the saturated hydraulic conductivity of $2x10^{-5}$, $1.5x10^{-5}$, and $6.5x10^{-5}$ $m.s^{-1}$, respectively, as estimated using field infiltration tests. The retention curves were obtained from the data measured in the overpressure apparatus. Meteorological data were measured in a meteorological station. Soil water tension was measured in-situ using water tensiometers. More information on the experimental area can be found in references (Pražák et al., 1994; Tesař, Šír, 1998).

Methods

Phytomass productivity was simulated using the RETU model (Tesař et al., 2001). The RETU model consists of three sub-models as follows. (1) The soil water movement including the water uptake for plant transpiration was modelled using the one-dimensional Richards' equation with a sink-term (Vogel et al., 1996). (2) The potential transpiration was calculated with the help of theory published by Pražák et al. (1994). The actual transpiration is equal to the potential transpiration if the suction pressure in the root horizon is higher than the limit value (in our case about –60 kPa), and to zero if the suction pressure in the root horizon falls below the limit value. Comprehensive discussion concerning this concept was brought by Novák & Havrila (2006). (3) The phytomass productivity is supposed to be proportional to the time of maximal production, defined as a sum of time intervals in which the vegetation temperature is equal to the optimum value. If the actual transpiration is less than the potential one, then the time of maximal production is less than its potential value.

The RETU model inputs are: meteorological quantities (the time course of precipitation, air temperature and global radiation), soil hydrophysical properties (retention curve and saturated hydraulic conductivity of each soil horizon), and plant cover (albedo and optimum temperature for plant growth). The RETU model outputs are: the time course of water infiltrated in the soil, water stagnant on the soil surface, water in surface runoff, water extracted from the soil for actual transpiration, water drained from the soil into subsoil horizons, suction pressure and soil moisture in individual soil horizons, latent heat used for transpiration, sensible heat emitted from the plant cover into the atmosphere, vegetation temperature, and phytomass productivity. The RETU model inputs and outputs have a clear physical meaning and can be experimentally evaluated (Tesař et al., 2001).

Results

The phytomass productivity was simulated using the RETU model at the site Zábrod – field for three growing seasons with the same duration from May 1 till September 30 (Table 1). The optimum temperature for plant growth was changing from 22 to 28ºC, and the phytomass productivity was simulated using the meteorological data corresponding to the natural conditions. The 1987 season is representing the long-term mean season. The 1992 season was the driest and warmest season, and the 1995 season was medium in temperature and uncommonly rich in precipitation. At the end of the 1995 season, the soil water content was in about 50 mm higher than at its beginning. While the 1987 and 1995 seasons represent two typical variants of a heat-controlled hydrologic cycle, the 1992 season represents an extreme variant of water-controlled hydrologic cycle.

Potential transpiration determined by the sub-model of plant transpiration in all three seasons (Table 2) revealed a strong dependence of the potential transpiration PET (mm/growing season) on the optimum temperature for plant growth. It can be stated that the optimum temperature rise in 1ºC can increase the potential transpiration in about 15%. This means that both the potential transpiration and hydrologic cycle are very sensitive to the optimum temperature for plant growth.

Table 1: Climatic characteristics of growing seasons.

Growing season	1987	1992	1995
Duration	15.5.–30.9.	27.5.–30.9.	27.5.–30.9.
Number of days	139	127	127
Precipitation sum (mm)	372	204	544
Potential transpiration sum (mm)	178	360	222
Mean daily potential transpiration (mm/day)	1.28	2.83	1.75
Mean air temperature (ºC) from 5 a.m. till 8 p.m.	11.7	14.3	12.1
Global radiation sum (kWh m^{-2})	600	764	643

Table 2: Simulated potential transpiration as a function of the optimum temperature for plant growth.

Growing season	Potential transpiration (mm) at the optimum temperature						
	22ºC	23ºC	24ºC	**25ºC**	26ºC	27ºC	28ºC
1.5.–30.9.1987	261	233	204	**178**	154	132	112
1.5.–30.9.1992	508	456	406	**360**	317	278	241
1.5.–30.9.1995	336	298	264	**232**	203	177	153

Let us to analyse the sensitivity of potential production time on the optimum temperature for plant growth providing that water is not a factor limiting plant transpiration (i.e. heat-controlled hydrologic cycle). Potential production time PPT for all the three seasons and the optimum temperatures from 22 to 28 ºC are shown in Table 3 in hours per season. It can be stated that the mean PPT is about 3–7 hours a day. Vegetation is sub-cooled during remaining time. Heat scarcity

is the growth limiting factor in a cold climate as it can be seen in Table 3 where the optimum temperature increase in 1ºC results in the PPT drop in about 10% in 1987, 7% in 1992, and 9% in 1995. The 1992 PPT was 162%, and the 1995 PPT was 110% of the potential production time in 1987 for all the values of optimum temperature.

Table 3: Simulated potential production time as a function of the optimum temperature for plant growth.

Growing season	Potential production time (hours) at the optimum temperature						
	22ºC	23ºC	24ºC	**25ºC**	26ºC	27ºC	28ºC
1.5.–30.9.1987	738	680	625	**570**	517	465	418
1.5.–30.9.1992	1134	1061	989	**923**	860	794	726
1.5.–30.9.1995	809	743	683	**626**	573	523	468

Let us to extend the above-mentioned analysis providing that water can be the factor limiting plant transpiration (i.e. the heat-control of hydrologic cycle was replaced by the water-control of hydrologic cycle). The actual transpiration ET is considered to be zero in the case when the tensiometric pressure in the root zone of soil is less than –60 kPa, and ET = PET in other cases. The ratio ET/PET (Table 4) shows the degree in which water demands of the vegetation cover were supported in the seasonal scale. The actual production time (Table 5) was calculated using the ratios ET/PET (Table 4) and potential production time (Table 3). In this approach, the actual production time means duration of the optimum temperature for plant growth, and it is less than the potential production time in the periods, in which the plants are heated over the optimum temperature.

The ratio ET/PET in the long-term mean season 1987 (Tables 4 and 5) shows that the actual production time is not reduced in comparison with the potential one. It means that the plants are not heated over the optimum temperature and the hydrologic cycle is heat-controlled during the whole vegetation season for each optimum temperature for plant growth between 22 and 28ºC. In the 1995 season (medium in temperature and rich in precipitation), a decrease in the production time due to water scarcity is less important (Tables 4 and 5). It means that heat scarcity is the main limiting factor for plant growth in the season medium in temperature and sufficient in precipitation. But the importance of water control increases with the drop in optimum temperature below 25ºC. In the driest and warmest season 1992, the actual production time was reduced considerably due to water scarcity. Due to an overheating, 28–55% of the potential production time was lost. It means that water scarcity is the limiting factor of plant growth in a dry season.

Table 4: Simulated ET/PET (%) as a function of the optimum temperature for plant growth.

Growing season	ET/PET (%) at the optimum temperature						
	22ºC	23ºC	24ºC	**25ºC**	26ºC	27ºC	28ºC
15.5.–30.9.1987	100	100	100	**100**	100	100	100
15.5.–30.9.1992	45	50	54	**59**	63	67	72
15.5.–30.9.1995	84	87	90	**93**	94	95	95

Table 5: Simulated actual production time as a function of the optimum temperature for plant growth.

Growing season	Actual production time (hours) at the optimum temperature						
	22ºC	23ºC	24ºC	**25ºC**	26ºC	27ºC	28ºC
1.5.–30.9.1987	738	680	625	570	517	465	418
1.5.–30.9.1992	510	531	534	**545**	542	532	523
1.5.–30.9.1995	680	646	615	582	538	497	445

Discussion

Based on the natural selection hypothesis, the temperature of 25ºC was found to be the optimum temperature for plant growth in the studied site because (1) no hydrologic extreme which could threaten plant surviving was met in all vegetation seasons, and (2) the highest production was reached at this temperature even in the critically dry season 1992 (Table 5). The optimum temperature of 25ºC is in a good agreement with the value of 23–24ºC obtained from the direct measurement of optimum temperature for plant growth in a cold climate (Körner & Larcher, 1988; Körner, 2003).

Spiecker (1995) concluded that the growth of Norway spruce in Black Forest (Germany, elevation about 900–1200 m a.s.l.) strongly correlates with precipitation and air temperature. High air temperature and low precipitation during the vegetation period reduce growth rate even in that area where average precipitation is high and average air temperature is relatively low. This finding supports our conclusion that the growing season with water-controlled hydrologic cycle is critical for plant growth in a cold climate. In lower altitudinal vegetation zones (600-650 m a.s.l.) there are climatic risks for spruce stands still dangerous (Grabařová & Martinková 2002).

Co-evolution of plants, soil cover and climate on the whole Earth simulated Kleidon (2006). He concluded that optimum conditions for maximum productivity are close to the present day climatic conditions. In the case of lower optimum temperature for plant growth, higher consumption of water for transpiration could result in a depletion of water source, increase in plant temperature owing to a drop in transpiration, and finally in a reduction or cessation of plant growth as a consequence of the high temperature of plant. In the case of higher optimum temperature for plant growth, the heat from solar radiation is not sufficient for heating up the plants to this temperature, resulting in a reduction or cessation of plant growth as a consequence of the low temperature of plant. The optimum temperature of 25ºC for plant growth in the present day conditions in the cold climate areas can lower both risks of reduction or cessation of plant growth, and is an effective compromise between the optimum temperature for plant respiration (about 30–35°C) and the optimum temperature for type-C3 photosynthesis (about 18–22°C), where a good solubility of CO_2 in water is necessary (Brdička, Dvořák 1977, Larcher 2003).

Conclusions

It was found from the monitoring of hydrological cycle in the studied mountain localities in the Czech Republic and simulation of the phytomass productivity at the experimental area Zábrod – field that the optimum temperature for plant growth is 25ºC, and the plants having this optimum temperature produce the biggest volume of phytomass in the long-term scale.

Acknowledgement

The authors thank Dr. Viliam Novák (Institute of Hydrology, Slovak Academy of Sciences, Bratislava, Slovakia) for his valuable comments to the manuscript. The research has been supported by the Academy of Sciences of the Czech Republic (Institutional Research Plan AV0Z20600510 and Project No. 1QS200420562), Grant Agency of the Academy of Sciences of the Czech Republic (Project No. IAA3042301) and Grant Agency of the Czech Republic (Project No. GA205/05/2312). Additional support from the Scientific Grant Agency VEGA Project No. 2/6003/26 and MSM 621 564 8902 is greatly acknowledged.

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