Evaluation of productivity at the leaf level of juvenile poplars

P M Evlakov¹, AP Tsarev, R P Tsareva, S G Rzhevsky and V Yu Zapletin

All-Russian Research Institute of Forest Genetics, Selection and Biotechnology, 105 Lomonosova street, 394087 Voronezh, Russia

¹E-mail: peter.evlakov@yandex.ru

Abstract. The purpose of this research was the comparative study of the morphological traits of the poplars assimilation apparatus and their possible use in the selection process. Leaf area, not leaf length, was taken as a unit of the plastochronic index for the first time in this work. Analysis of the sigmoidal curve of the growth of the fifth leaf of the apical shoot of poplar showed that 80% of the maximum leaf surface is reached through an interval of 2.2 plastochrons and corresponds to the 20-day calendar age of the leaf. It is noted that the raw biomass of the cross-section poplar ‘Hybrid e.s.-38’ was significantly higher than in other compared varieties. Two groups of genotypes with a high and a low specific surface leaf density were identified. Average size of the leaf area, as well as the total amount of the assimilating surface of the apical shoot of the poplar ‘Hybrid e.s.-38’, 2 and more times exceeded the similar parameters of the poplars studied. Such changes in the current increment and age dynamics of the photosynthetic apparatus of the cross-section ‘Hybrid e.s.-38’ allow to recommend it in breeding as a parent material for creating promising varieties of poplars.

1. Introduction

Poplar trees are used for the needs of the accelerated cultivation of wood for the production of biomass for bioenergy, fodder, chemical processing and other wood needs. Research and projects in poplar breeding have been intensified over recent decades and they are conducted under the auspices of the FAO International Poplar Commission as well as at the national level of individual countries [1-6]. Special emphasis is put on the studies of mini-rotational plantations with a short cutting (2-3 years) period [7-9]. Special focus is placed on the research into biomass yield and its energy value [10, 11], as well as the use of wood greens as feed additives for livestock [12, 13].

At the same time, the study of morphological structure and photosynthetic function at the first stages of ontogenesis has a significant importance for an early assessment of the suitability of biotypes for their use in the mini-rotational cultivation. In this regard, intensive search for express methods that will help evaluate and identify the most promising, the fastest growing clones and hybrids is being conducted.

Numerous experimental data on the morphological structure and photosynthetic function of various species of woody plants have been accumulated in the literature at the present time. In this connection intensive selection work and search for the criteria of a quick field express-test, which can reveal the fastest growing clones, hybrids, or species is being conducted [14-17].

Since more and more species, varieties and clones of poplar appear faster than their field tests have been passed, the criteria of fast and early selection of the best clones are needed [18, 19]. In fact, the use of early parameters for selection by breeders and physiologists will reduce the price and time of
The study of leaf traits and their relationship with growth and productivity is critical for improving poplar cultivation. Poplar species exhibit significant genetic variability in leaf traits and photosynthetic performance, which is essential for species selection and breeding programs. This research focuses on the determination of correlations between leaf traits and productivity, aiming to identify specific leaf area as a better integrative predictor of growth in poplars. The study's purpose is to determine if this trait can be used as a genetic indicator of productivity and to explore the role of photosynthetic carbon uptake in growth performance.

2. Materials and Methods
The objects of the research were promising hybrid and poplar varieties of the second year of life, belonging to different morphological and systematic sections (Table 1). The experimental objects were carried out on the juvenile site of the forest park of the Research Institute of Forest Genetics, Breeding and Biotechnology (Voronezh, European part of the Russian Federation). The climate is continental. The number of days with precipitation ranged from 140 to 170, the season duration of growing was 152 days, the growing season began from the middle to the end of April. The coldest months were January and February, the warmest ones – July and August. The absolute temperature minimum reached -38°C, the maximum was +40°C. Most of the annual amount of precipitation (60-70%, 314 mm) fell on a warm period. The average annual precipitation was from 450 to 550 mm.

In the spring of 2016, 25 cm long cuttings of poplars were planted for rooting and growth on the juvenile site of the forest park. At the end of the growing season, the height of seedling of various forms of poplars ranged from 33 to 97 cm (Table 1).

In 2017 the experiment was carried out in three replicates. In the second half of April, with the air temperature of 12-14 °C, the annual poplar plants from the entrenched section of the forest park of the Institute were transplanted into 2-litre and 20 cm height vegetation vessels. The experimental design included placing the plants in the experimental section 0.35 x 0.75 m.
Table 1. Characteristics of the promising biotypes of poplars planted on the territory of the forest park section of the “Research Institute of Forest Genetics, Breeding and Biotechnology”.

| #  | Name             | No. | Height of shoots, cm | Author of hybrid          |
|----|------------------|-----|----------------------|---------------------------|
| I. Durig poplars |                 |     |                      |                           |
| 1  | ‘Volostistoplody’| 45  | 97                   | View [3]                  |
| II. Black poplars with branchy form of crown |     |     |                      |                           |
| 2  | ‘Regenerata’     | 90  | 50                   | Euro-American Hybrid [3]  |
| III. White poplars with pyramidal crown shape |     |     |                      |                           |
| 3  | ‘Veduga’         | 26-07 | 45                 | Tsarev AP [3]            |
| IV. Black poplars with pyramidal crown shape |     |     |                      |                           |
| 4  | ‘Pioneer’        | 42  | 29                   | Apple AS [3]              |
| V. Intersectional Hybrids |     |     |                      |                           |
| 5  | ‘Hybrid e.s.-38’ | 94  | 38                   | Veresin MM [3]            |
| V. White poplars with pyramidal crown shape |     |     |                      |                           |
| 6  | ‘Veduga*’        | 26-07 | 33                 | Tsarev AP [3]            |

* – microclonally propagated (in vitro) variety ‘Veduga’.

To reduce the overwarming of the substrate in hot summer conditions, the vegetation vessels were buried in the soil, which made it possible to create microclimatic conditions close to the soil. The bog neutralized peat brand “Agrobalt-N” (pH 6.3, ash mass fraction 7.7%) was used as a substrate. The finished substrate was adjusted to a moisture content of 60-70% by irrigation and thorough mixing. Throughout the vegetation period, planned maintenance, watering, weeding and feeding of all 6 forms of poplars were carried out. The need for wel3.1-timed morning irrigation was determined by vessels weighing. The humidity of the substrate was maintained at 60-70% of its water capacity. The application of complex mineral fertilizers started from the 5th week after planting and continued throughout the rapid growth phase.

The area of the leaf surface of the apical shoot without leaf separation from the plant was determined by an improved measurement technique using a digital camera [27]. The method was based on the calculation of the proportion of the area using the number of pixels forming the leaf image and the square of known area in one picture using software Corel PhotoPaint.

The specific surface density of the leaf, which characterizes the ratio of the dry weight of the leaf to its area, was determined by weighing each of 10 even-aged leaves of apical shoot separately. Leaf and shoot biomass have been obtained by using analytical scales of the Ohaus PA214C brand (USA). The weight of the apical shoot at the end of the growing season was assumed to be equal to their annual production or weight gain. The productivity of 1 dm² of the apical shoot leaf area during growing season [g/dm²·year⁻¹] was calculated by dividing the annual increase of dry weight (g) by its assimilating leaf area. The calculated value approximately matched the net CO₂ assimilation rate (NAR) of poplar shoot over the studied period, as defined by Blackman and Wilson [27].

The choice of the apical shoot in poplar plants as an object of research was the best option characterizing the photosynthetic function of the plant assimilation apparatus, since the leaves of the
upper layer have a more effective influence on the height growth of the two-year-old Populus hybrids than the leaves of the lower layer [23].

In our case, the age of the leaf was expressed not chronologically, but through the number of plastochrons, i.e. intervals separating the set of two consecutive leaves or the passing of these leaves of the same phase of formation [28-30]. By analogy with the Finnish researcher Kaibeyainen EL, who took as one leaf plastochrone index a leaf, which under optimal conditions had a positive gas exchange, i.e. the intensity of photosynthesis began to exceed the intensity of respiration [14]. In our case, the leaf area equal to 4 cm² was taken as a unit of the plastachrone index.

In order to identify the optimal for measuring the rate of visible photosynthesis morphological leaf traits of poplar plants, the growth dynamics of apical shoot leaf of the intersectional ‘Hybrid e.s.-38’ have been analyzed. It is known that leaves of the upper tier of two-year poplar hybrids have more efficiency on the height growth than leaves of the lower tier [23].

The obtained data were processed using statistical methods of the software Statistica. For most traits, the errors of arithmetic means were 5-10%.

3. Results and discussion

The sigmoidal curve shown in figure 1 is a graph of the formation of the fifth leaf of the apical shoot of poplar ‘Hybrid e.s.-38’ over the area of the leaf blade. Analysis of the curve allows us to determine the age of the leaf, corresponding to a specified (80%) size of the leaf area.

![Figure 1](image)

**Figure 1.** The growth of the fifth leaf of the apical shoot is exemplified by the poplar ‘Hybrid e.s.-38’: a) leaf calendar age in days; b) leaf age expressed in plastochrons (LPI); T – leaf age corresponding to an area of 80% of the maximum.

According to the literature data, for most broad-leaved trees the maximum magnitude of visible photosynthesis is detected somewhat earlier than the leaf reaches its maximum size. So, for poplar plants, this value corresponds to 80% of the maximum area of the leaf blade.

In our case, the point T corresponds to the calendar age of the leaf of the apical shoot of 20 days (figure 1a). Estimating the leaf age by analyzing the growth curve has the disadvantage that the temporal growth rates do not correlate with the overall growth and morphogenesis of the whole plant [30]. To overcome this disadvantage, the course of leaf growth is represented by the number of plastochrons, i.e. intervals separating the set of two consecutive leaves or the passing of these leaves of the same formation phase (figure 1b). Using the example of the fifth leaf of the apical shoot of poplar, it is shown that 80% of the maximum leaf surface is reached through an interval of 2.2 plastochron. For the standard passage of plastochron, the area equal to 4 cm² is conventionally accepted. In the future, when studying the varietal features of the photosynthetic apparatus in different poplar genotypes, we will use leaves of the upper layer at the age of 20 days (leaf plastochronic index
of 2.2-4.4). For example, on June 20, the area of leaf #10 was 85.1 cm², and that of sheet No. 11 was 31.0 cm². The plastochron shoot index was 12.77 – the number of elementary cycles (plastochrons) that the shoot passed through by the time of its age estimation. The plastochron index for this leaf was 2.77.

The current increment in dry matter of the apical shoot of biennial poplar plants belonging to different morphological and systematic sections is shown in table 2. A comparative analysis of the data presented in table 2 showed that the raw biomass of the apical shoot in the cross-section poplar 'Hybrid e.s.-38' significantly exceeds the analogous figures of the compared variety samples. The main contribution to the biomass of the apical shoot (24.6 ± 2.74 g) is made by the raw weight of the leaf (18.7 ± 1.98 g), which is 76% of the total biomass of the apical shoot. An analogous trend is observed when comparing the current increment of dry matter in the apical shoot in different poplar genotypes. A detailed analysis of the results allows us to distinguish two groups of analyzed hybrids and varieties. In the first group with high biomass of the apical shoot, three forms of poplar can be attributed: 'Hybrid e.s.-38', 'Pioneer' and 'Veduga*', which are characterized by high growth rates during the vegetation period. Relatively low rates of growth are representative of poplars 'Volosistoplodny', 'Regenerata' and 'Veduga'. Large variations in biomass, functional and structural indicators that determine productivity, were also observed among poplars [22], which corresponds to the results of the study revealed.

Table 2. Increase of apical shoot in different poplar varieties.

| Option        | Raw weight, g | Dry weight, g | Leaf productivity, g/dm² year⁻¹ |
|---------------|---------------|---------------|---------------------------------|
|               | leaves  | steam | total  | leaves  | steam | total  |                                  |
| 'Volosistoplony'       | 5.8±1.10 | 2.4±0.89 | 8.2±1.98 | 2.0±0.28 | 0.9±0.28 | 2.9±0.55 | 1.45                             |
| 'Regenerata'            | 2.8±0.95 | 1.6±0.27 | 4.4±1.08 | 0.9±0.27 | 0.6±0.11 | 1.5±0.34 | 0.70                             |
| 'Veduga'                | 6.5±1.11 | 3.8±0.69 | 10.3±1.8 | 2.2±0.35 | 1.7±0.57 | 3.9±0.92 | 1.14                             |
| 'Pioneer'               | 10.2±3.09 | 6.2±2.18 | 16.4±5.27 | 3.2±0.89 | 2.8±0.97 | 6.0±1.85 | 1.21                             |
| 'Hybrid e.s.-38'        | 18.7±1.98 | 5.9±0.76 | 24.6±2.74 | 5.5±0.54 | 2.6±0.32 | 8.1±0.85 | 0.93                             |
| 'Veduga*'              | 10.6±1.14 | 8.0±0.22 | 18.6±1.27 | 3.7±0.38 | 3.3±0.04 | 7.0±0.38 | 1.07                             |

However, it should be noted that the productivity per unit area of the leaf of the apical shoot during the vegetation period provided the maximum increase in biomass to the species of the poplar 'Volosistoplodny' (1.45 g/dm² year⁻¹).

Morphometric parameters of the studied varieties and hybrids of poplar of the second year of life are presented in table 3. Leading positions in terms of the current increment in apical shoots in height, significantly exceeding the analogous indicators of the poplar genotypes studied, are taken by the microclonally propagated variety 'Veduga*'. The share of the current increment in height is 60% of the size of the plant at the end of vegetation (109.3 ± 3.18 cm). The following varieties and hybrids showed the minimum current increment during the vegetation period: 'Regenerata' (20.7 ± 2.03 cm), 'Volosistoplodny' (42.0 ± 8.50 cm) and 'Hybrid e.s.-38' (43.7 ± 4.26 cm). The white poplar with the pyramidal crown form 'Veduga' and the representative of the 'Pioneer' section of black poplars occupy the middle position among the analyzed poplar genotypes in terms of the current increment (50 and 51 cm respectively). Dillen et al., who studied the diversity of leaf traits related to the productivity in 31 Populus deltoides × Populus nigra hybrids, showed that the stem length differed significantly in annual plants with containerized root system [23]. The best index of productivity per unit area of the leaf, as in the analysis of the current growth, during the vegetation period showed balsamic poplar.
"Volosistoplodny" (table 3). The second position on this feature is occupied by the representative of Lombardy poplars hybrid "Pioneer", as well as the white poplar 'Veduga'.

**Table 3. Morphometric characteristics of different poplar varieties**

| Option          | Height of a plant at vegetation, cm | Current increment of apical shoot in height, cm | Share of current increment in height, % | Sheet productivity cm/dm²/year<sup>1</sup> |
|-----------------|--------------------------------------|-----------------------------------------------|----------------------------------------|------------------------------------------|
|                 | beginning | end                                      |                                        |                                         |
| 'Volosistoplodny' | 68.0 ± 2.52 | 106.7 ± 6.49                            | 42.0 ± 8.50                            | 36 ± 3.0                                | 1.97                        |
| 'Regenerata'     | 58.3 ± 5.04 | 79.0 ± 7.00                             | 20.7 ± 2.03                            | 26 ± 1.0                                | 0.97                        |
| 'Veduga'         | 59.7 ± 1.20 | 109.7 ± 1.45                            | 50.0 ± 2.65                            | 46 ± 2.0                                | 1.45                        |
| 'Pioneer'        | 39.3 ± 3.67 | 90.3 ± 12.99                            | 51.0 ± 9.45                            | 56 ± 3.0                                | 1.03                        |
| 'Hybrid e.s.-38' | 46.3 ± 1.45 | 90.0 ± 3.00                             | 43.7 ± 4.26                            | 48 ± 3.0                                | 0.50                        |
| 'Veduga *'       | 43.3 ± 2.40 | 109.3 ± 3.18                            | 66.0 ± 2.08                            | 60 ± 2.0                                | 1.02                        |

Along with the analysis of the current height and biomass increment of the apical shoot, we analyzed the morphometric characteristics of the leaf of the apical shoot of various forms of poplar (table 4). It was reliably shown that the thinnest leaves were recorded in white poplars of the variety 'Veduga' and 'Veduga*'. The maximum thickness of the leaf blade was observed in the inter-sectional 'Hybrid e.s.-38' and the representative of the balsam poplar 'Volosistoplodny' (193.9 ± 2.27 and 188.9 ± 2.68 mm, respectively).

The leaf area of the cross-sectional poplar 'Hybrid e.s.-38' ("Voronezh Giant") significantly exceeded the same parameters for all tested varieties and poplar hybrids. More than 3 times compared with 'Voloshistoplodny' and 1.5 times compared with the variety 'Pioneer'.

Specific surface density of the leaf (SSD), which is an integral indicator of the mesostructure of the leaf and it characterizes the photosynthetic feature of the genotype for the assimilation of carbon dioxide in optimal conditions for the growth of the species. This characteristic combines all the internal and external properties of the assimilating organs of the plant [31]. The value of the SSD leaf has genetic conditioning and it differs in different genotypes [32].

**Table 4. Morphological characteristics of the leaf of apical shoot of various forms of poplar.**

| Option            | Thickness, Micron | Area, cm² | Weight of 1 dm² Sheet, g | Weight of 1 sheet, mg |
|-------------------|-------------------|-----------|--------------------------|-----------------------|
|                   | Raw               | Dry (SSD) | Raw                      | Dry                   |
| 'Volosistoplodny' | 188.9±2.68        | 17.0±1.43 | 1.29±0.0025              | 0.48±0.028            | 218±18.0               | 46±3.3                |
| 'Regenerata'      | 156.7±3.37        | 27.9±1.95 | 1.33±0.013               | 0.41±0.007            | 372±27.0               | 90±5.7                |
| 'Veduga'          | 113.8±0.65        | 29.1±1.02 | 1.93±0.034               | 0.37±0.009            | 561±23.3               | 151±1.2               |
| 'Pioneer'         | 163.8±3.24        | 38.7±1.62 | 1.34±0.026               | 0.46±0.014            | 518±25.8               | 113±5.7               |
| 'Hybrid e.s.-38'  | 193.9±2.27        | 56.3±2.42 | 1.65±0.050               | 0.48±0.020            | 924±43.1               | 195±0.6               |
| 'Veduga *'        | 119.7±0.89        | 28.6±1.72 | 1.38±0.072               | 0.34±0.007            | 391±23.1               | 115±5.3               |
Based on the results presented in table 4, a group of genotypes with a high specific surface leaf density (0.46-0.48 g / dm²) can be distinguished: ‘Hybrid e.s.-38’, ‘Volosistolodny’ and ‘Pioneer’, as well as a group with a low specific surface density, which includes white poplars with a pyramidal crown of the ‘Veduga’ variety (0.34-0.37 g / dm²). The large clonal variability of a fully formed leaf of poplars is shown by Dillen et al. [23]. Thus, dense or thick leaves are characteristic of high-yielding poplar clones.

Although photosynthetic carbon absorption does not always correlate with productivity, the formation of a leaf surface can be the best integral indicator of growth processes. The area of a single leaf, as well as the area of the assimilating surface of a plant, can be a promising indicator that determines the potential productivity of a species [20, 22].

In comparative studies of various characteristics in different genotypes of woody plants, it is advisable to use leaf area indicators that are fairly resistant to various environmental conditions and are easily controlled. Consequently, these characteristics are very well matched with molecular markers, and can be used in poplar breeding [19].

In connection with this, we analyzed the age dynamics of the average leaf area and the assimilation surface of the apical shoot in different systematic forms of poplar of the second year of life (figures 2 and 3).

Based on the data presented in figure 2, it can be seen that throughout the vegetative period, the average size of the poplar leaf ‘Hybrid e.s.-38’ was significantly higher compared to other poplar varieties. Thus, at the time of measuring the varietal features of the intensity of photosynthesis and transpiration in different poplar genotypes, the average area of the leaf was 42.4 ± 6.11 cm², which is 2 and more times higher than the analogous index of the poplars [33]. In contrast, a large number of leaves in combination with smaller sizes is characteristic of the balsam poplar ‘Volosistolodny’ (9.7 ± 1.39 cm²) (figure 2).

The size of poplar leaves usually decreases, while the number of leaves increases from a moderate to an arid environment (that is, from a moderate wet to dry climate, respectively). A large number of leaves in combination with smaller sizes can be an adaptive feature, as well as an adaptive response in droughty environmental conditions. In contrast, larger and sparse leaves are probably preferable in temperate climate, where sunny days are often followed by gloomy days [34, 35].

![Figure 2. Ontogenetic dynamics of the average leaf area of apical shoots in different systematic forms of poplar of the second year of life.](image1)

![Figure 3. Ontogenetic dynamics of the growth of the assimilative surface of the apical shoot in various systematic forms of the poplar of the second year of life, 2017.](image2)
Throughout the period of vegetation, the age dynamics of the growth of the assimilation surface of the apical shoot in various systematic forms of poplar had a sigmoidal form of dependence (figure 3). Total leaf area was positively correlated to the maximum individual leaf area during plant ontogenesis.

The most intensive growth of the leaf assimilation surface was observed in the phase of intensive growth of poplar plants (from 05.06 to 01.08). A slight increase in the assimilation surface in all tested genotypes in the second and third weeks of May (May 5-19) is probably due to a slight decrease in the temperature of the atmosphere compared to the average multi-year temperature of 7.4 °C.

A comparative analysis of the ontogenetic dynamics of average leaf area, total leaf area and productivity of the apical shoot of various systematic forms of the poplar of the second year of life demonstrates close relationship between analyzed traits. A similar conclusion was reached by Bunn et al. who studied leaf-level productivity indicators for poplars growing in the UK in short rotation crops [19].

It is known that the individual development of a poplar leaf is very sensitive to abiotic factors. Inside the tree crown, the characteristics of a single leaf vary from the temperature, the lighting conditions of the layer in which it is located [36].

4. Conclusion
Leaf area, not leaf length, was taken as a unit of the plastochronic index for the first time in this work. As a result, the analysis of the sigmoidal curve of the formation of the fifth leaf of the apical shoot of poplar has shown that 80% of the maximum leaf surface is reached through the interval of 2,2 plastichrons and corresponds to the 20-day calendar age of the apical shoot. This work has showed that the fast-growing genotypes of poplars are characterized by a number of morphological traits at leaf level, which can be used in the selection process for high productivity. It has been found that the leaf area and summary assimilating leaf surface are the most important factors determining the formation of high productivity of juvenile poplars. The nature of the changes in the age dynamics of the leaf area and the assimilative surface of the apical shoot of the intersection ‘Hybrid e.s.-38’ allows us to recommend it for use in breeding as a source material for creating promising poplar varieties. The cross-sectional poplar ‘Hybrid e.s.-38’ is a preferable ‘ideotype’ for creating short rotation poplar plantations.

References
[1] Viart M 1979 Poplars and Willows in Wood Production and Land Use (Rome: Food and Agriculture Organization of the United Nations) p. 328
[2] Isebrands J S and Richardson J 2014 Poplars and Willows: Trees for Society and the Environment (Ontario: FAO of the United Nations and CABI) p. 634
[3] Tsarev A P 1986 Cultivarology of Poplar (Voronezh: Voronezh University) [in Russian] 152 p
[4] Tsarev A P 2010 World experience of plantation cultivate Scholarly Memoirs of Petrozavodsk State University [in Russian] 6 (111) 42
[5] Tsarev A, Wühlisch von G and Tsareva R 2017 Hybridization of poplars in the central chernozem region of Russia Silvae Genetica 66 10
[6] Fladung M and Wühlisch G 2018 Improving productivity, resistance, and adaptability in poplar – development of genetic markers for aspen (MaRusiA) Thünen Report 62 9
[7] Tsarev A P and Mironenko S S 1997 Possibilities of poplar energetic plantations in Central forest-steppe Forestry [Lesnoje Hosjajstvo – in Russian] 2 35
[8] Hoffmann M 2005 Pappeln als nachwachsender Rohstoff auf Ackerstandorten – Kulturverfahren, Ökologie und Wachstum unter dem Aspekt der Sortenwahl. Hann. (Münden: Schriften des Forschungsinstitutes für schnellwachsende Baumarten) [in German] p. 145
[9] Meyer M, Gebauer K, Janssen A and Krabel D 2018 The importance of fuel characteristics of poplars and aspens (Populus spp.) from German short rotations and Russian forests Thünen Report 62 61
Wühlisch von G 2006 Ergebnissen der Züchtung von Pappeln und Aspen in Großhansdorf. Perspektiven für die Energie – und Rohstoffezeugung Vortr. Pflanzenzüchtung [in German] 70 157

Tsarev A P and Tsarev V P 2015 Biomass of subgenus Eupopulus Dode poplars for bioenergy production Forest bulletin – Bulletin of Moscow State Forest University [Lesnoy Vestnik – in Russian] vol 19(6) 57

Tsarev A P 2010 Amino acids composition and fodder value of poplar leaves at minirotation cultivation. Proc. 5th Int. Poplar Symposium Poplars and Willows “From Research Models to Multipurpose Trees for a Bio-based Society” (Orvieto, Italy) p. 135

Tsarev A P 2012 Fodder Value of Populus euramericana green biomass J. Agr. Sci. Tech. 2(5) 498

Kaiheinen E L 2009 Parameters of the light curve of photosynthesis in Salix dasyclados and their variation during vegetation. Russ. J. Plant Physiol. [Fiziologiya Rasteny – in Russian] 56(4) 490

Kaiheinen E L and Pelkonen P 2007 Optimization of photosynthesis and transpiration in unseparated willow leaves on plantations of rapid renewal Russ. J. Plant Physiol. [Fiziologiya rasteniy – in Russian] 54(3) 350

Verlinden M S, Broeckx L, S Bulcke van den J, Acker van J and Ceulemans R 2013 Comparative study of biomass determinants of 12 poplar (Populus) genotypes in a high-density short-rotation culture Forest Ecol. Manag. 307 101

Broeckx L S, Fichot R, Verlinden M S and Ceulemans R 2014 Seasonal variations in photosynthesis, intrinsic water-use efficiency and stable isotope composition of poplar leaves in a short-rotation plantation Tree Physiol. 34 701

Gordon J C and Promnitz L C 1976 Photosynthetic and enzymatic criteria for the early selection of fast-growing Populus clones Tree physiology and yield improvement. Eds Cannell M G R, Last F T (London: Academic Press) pp. 79-97

Bunn S M, Rae A M, Herbert C and S Taylor G 2004 Leaf-level productivity traits in Populus grown in short rotation coppice for biomass energy Forestry 77 307

Ceulemans R, Scarascia-Mugnozza G, Wiard B M, Braatne J H, Hinckley T M, Stettler R F, Isebrands J G and Heilman P E 1992 Production physiology and morphology of Populus and their hybrids grown under short rotation. I. Clonal comparisons of 4-year growth and phenology Can. J. For. Res. 22 1937

Navarro A, Portillo-Estrada M, Arriga N, Vanbeveren S P and P Ceulemans R 2018 Genotypic variation in transpiration of coppiced poplar during the third rotation of a short-rotation bio-energy culture GCB Bioenergy 10(8) 1

Marron N, Dillen S Y and Ceulemans R 2007 Traits for indirect selection of high yielding poplar hybrids Env. Exp. Bot. 61 103

Dillen S Y, Rood S B and Ceulemans R 2010 Growth and Physiology Genetics and Genomics of Populus. Plant Genetics and Genomics: Crops and Models vol 8 Eds: Jansson S, Bhalearo R, Groover A (New York: Springer) 39

Allwright M R, et al. 2016 Biomass traits and candidate genes for bioenergy revealed through association genetics in coppiced European Populus nigra (L.) Biotechnol. Biofuels 9 195

Sivolapov A I, Politov D V, Mashkina O S, Belokon M M, Sivolapov V A, Belokon Y S and Tabatskaya T M 2014 Cytological, Molecular-Genetic and Silvicultural-Selection Research of Polyploid Poplars Siberian Journal of Forest Science [Sibirskiy Lesnog Zhurnal – in Russian] 4 50

Le Gac A, et al. 2018 Winter-dormant shoot apical meristem in poplar trees shows environmental epigenetic memory J. Exp. Bot. 69(20) 4821

Dmitriev N N and Khushnidinov Sh K 2016 Method of accelerated determination of the leaf surface area of agricultural crops using computer technology Bulletin of KrasGAU, Biological Sciences [Vestnik KrasGAU, Biologicheskiy Nauki – in Russian] 7 88
[28] Tselnicker Y L 1978 Physiological basis of shade tolerance of woody plants [in Russian – Fiziologicheskiye osnovy tenevynoslivosti drevesnykh rasteniy] (Moscow: Nauka) p.215
[29] Erickson R O and Michelini F I 1957 The plastochron index Amer. J. Bot. 44(4) 297
[30] Mokronosov A T 2006 Photosynthesis. Physiological, ecological and biochemical aspects [in Russian] (Moscow: Academy) p. 448
[31] Slemnev N N 1996 Features of photosynthetic activity of Mongolia plants: evolutionary, ecological and phytocenotic aspects Russ. J. Plant Physiol. [Fiziologiya rasteniy – in Russian] 43 (3) 418
[32] Mirakilov H M and Giasidinov B B Abdullayev H A Karimov H H Soliiyeva B A Ergasheva E A Kasparova I S 2013 Specific surface density of a sheet of old-fashioned and modern varieties of fine-fiber cotton Reports of the Academy of Sciences of the Republic of Tajikistan [Doklady AN respubliki Tadzhikistan] 56(3) 250
[33] Evlakov P M, Tsarev A P and Zapletin V Yu 2017 Study of photosynthetic features and intensity of transpiration in various varieties and poplar clones (Populus L.) Proceedings of the St. Petersburg Institute of Forestry [Trudy Sankt-Peterburgskogo NII lesnogo khozyaystva – in Russian] 4 4
[34] Dunlap J M, Heilman P E and Stettler R F 1995 Genetic variation and productivity of Populus trichocarpa and its hybrids. VIII. Leaf and crown morphology of native P. trichocarpa clones from the four river valleys in Washington Can. J. Forest Res. 25 1710
[35] Pearce D W, Millard S, Bray D F and Rood S B 2005 Stomatal characteristics of riparian poplar species in a semi-arid environment Tree Physiol. vol 26 pp 211–218
[36] Amelin A V, Fesenko A N, Chekalin Y I and Zaikin V V 2016 Photoenergy potential – Klondike in breeding Selection, Seed-growing and Genetics [Selektsiya, semenovodstvo i genetika – in Russian] 6 36