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Water availability effects on growth and phenology of 11 poplar cultivars growing in semiarid areas in Turkey

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Abstract
In Turkey, current wood production does not meet the demand of wood-products, and this gap is expected to be larger in the near future. It is necessary to increase the productivity and growth efficiency of current forests and to expand the extension of forest plantations, including areas where drought is the main climatic constraint. Even though researchers are currently working on hybridization programs to improve the quality and productivity of poplar cultivars, there are still large gaps in the understanding of the effects of drought on the performance and physiology of these cultivars. We analyzed the effects of water stress on growth and phenology of eight cultivars of black poplar (*Populus nigra*), two cultivars of the hybrid *P.* × *euramericana*, and one cultivar of eastern cottonwood (*P. deltoides*). The objective was to identify the cultivars better-adapted to dry conditions in semiarid areas of Turkey. Cuttings of the eleven cultivars were grown under two contrasting watering regimes (well-watered and water-stressed). Tree height and ground line diameter were periodically measured along with phenological traits such as bud break, leaf loss, and infection by *Cytospora chrysosperma*, a common fungal disease in Turkey. Results from this study may help forest managers select better-adapted poplar cultivars for semiarid conditions. According to our results, we consider that cultivars 'I-214' and 'Kocabey' may be adequate alternatives, and cultivars 'Ata-1', 'Gazi', and 'Geyve' may not be preferred for planting under water-limited areas in Turkey and similar regions of the Mediterranean basin.

Keywords Growth parameters · *Populus* · Water stress · Phenology · Cultivar selection

Introduction

Fast-growing species and hybrids of the *Populus* genus have a long history of cultivation to produce biomass that can be used as a source of lumber, fiber, fuel, and plywood. Additionally, poplars are valued for providing socio-environmental services such as shelter, soil

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protection, and water conservation, as well as for their use in phytoremediation, rehabilitation, and restoration of degraded ecosystems. Globally, the total area of planted poplars is about 31.4 million ha, of which 58% are managed for multi-purposes, 30% for wood production, 9% for environmental protection and 3% is managed for fuelwood production (FAO 2016). The International Poplar Commission (IPC) identified in 2016 the capacity of poplars to efficiently sequester carbon and contribute to the adaptation and mitigation of the effects of climate change. A contribution that could be achieved by afforestation and reforestation with appropriate species and cultivars adapted to various site conditions (FAO 2016).

Nowadays, about 18.3 million m^3 $year^{-1}$ of wood are harvested from Turkish forests, but the wood consumption of the country is about 29 million m^3 $year^{-1}$ (Velioğlu and Akgül 2016). The remaining 10.7 million m^3 $year^{-1}$ wood demand is being met by wood imports and by the establishment of industrial plantations with fast-growing species, including poplar trees, which is estimated to be about 3.7 million m^3 $year^{-1}$ (Velioğlu and Akgül 2016). In Turkey, industrial use of poplar wood (furniture, packing, particleboard, plywood, matches, etc.) has rapidly developed in recent years, reaching a consumption of about 2.1 million m^3 $year^{-1}$, which is mostly based on the wood of euramericana hybrid poplars. On the other hand, more than 80% of black poplar wood (1.6 million m^3 $year^{-1}$) is utilized as round wood for construction and fuel purposes by rural people (Tunçtaner 1998), mostly in semi-arid and barren regions of the country (Isık and Toplu 2004).

The productivity of poplar plantations depends highly on water availability, which is commonly ensured by irrigation. However, increasing irrigation costs, water shortages, and climate change models indicate an urgent need to find drought-tolerant or drought-resistant cultivars that can grow rapidly to maximize volume yield. This is especially important for the semiarid regions of Turkey, characterized by frequent periods of low rainfall that can produce summer drought conditions and significant soil water deficits. For example, annual average rainfall in Ankara was 376 mm during the 1995–2015 period, with 63% of it occurring during the winter and spring. Heatwaves above 34 °C are common during the summer months (Turkish Meteorological Service 2018, pers. comm.). These semiarid conditions are likely to increase in frequency and intensity (Kızılelma et al. 2015), hence, the growth and survival of poplar trees and other short-rotation species may decrease under climatic conditions in the near future.

In the Northern hemisphere, poplars are one of the most vulnerable tree species to drought (Pallardy and Kozlowski 1981). However, variations in drought resistance across species and interspecific hybrids have been reported (Strong and Hansen 1991; Tschaplinski et al. 1994; Souch and Stephens 1998; Brignolas et al. 2000; Monclus et al. 2006; Guet et al. 2015). The adaptation to weather extremes and drought conditions by poplar trees is regulated by adjustments to morphological and/or physiological traits, allowing trees to respond to changing climate and providing a mechanism for acclimation and adaptation (Bussotti et al. 2015). Therefore, understanding phenotypic plasticity to drought by poplar cultivars could improve the current extension of Turkish plantations toward areas where drought is the limiting factor.

Four poplar species occur naturally in Turkey; *Populus nigra* L., *P. alba* L., *P. tremula* L., and *P. euphratica* Oliv. (Stanton et al. 2014). To improve the quality and productivity of poplar plantations in Turkey, the Poplar and Fast Growing Forest Trees Research Institute (PRI) was created, almost 60 years ago, with the aim of introducing and testing exotic species and hybrids. Since 1962, numerous countrywide research studies and pilot plantations have been conducted by the PRI to select suitable cultivars of indigenous and exotic poplars for commercial plantations. As a result of these research studies, two cultivars among indigenous *P. nigra* were offered in 1965 to the International Poplar Commission (IPC) for international registration. The submitted cultivars were registered by the IPC as *P. nigra* cultivars ‘Anadolu’ and ‘Gazi’. Since then, these cultivars have been grown in nurseries and established in plantations in the Central, Eastern and South-eastern regions of Turkey, where the continental climatic conditions prevail. As a result of subsequent research conducted on around 300 clones, three new cultivars of indigenous *P. nigra* were selected and registered by the National Poplar Commission as ‘Behiçbey’ (hereafter named as ‘Behicbey’), ‘Geyve’ and ‘Kocabey’. Research results and field observations have shown that these new cultivars can be used in commercial plantations with comparable success as the two cultivars previously mentioned (Birler 2014*). P. nigra* cultivars ‘Ata-1’, ‘Çubuk-1’ (hereafter named as ‘Cubuk-1), and ‘Çubuk-2’ (hereafter named as ‘Cubuk-2), although not yet registered, have shown good field performance, having similar survival and productivity to the registered cultivars, and even outperforming them in semi-arid Central and continental Eastern Anatolia (Kahraman et al. 2011).

Exotic poplars were first introduced in Turkey in 1946, but they started being widely cultivated only after 1962, when materials and related information of the species *P. deltoides* W.Bartram ex Marshall, *P. maximowiczii* A. Henry, and *P. trichocarpa* Torr. & A.Gray ex. Hook. and the hybrid *P.* × *euramericana* (Dode) Guinier (*P. deltoides* × *P. nigra*) were introduced from several countries within the frame of research studies on poplar genetic and selection (Stanton et al. 2014). Based on results from studies on exotic poplars conducted by the Poplar Research Institute (Italy), the *P.* × *euramericana* cultivar ‘I-45/51’ was selected for harsh site conditions and with reduced management intensity, while the *P.* × *euramericana* cultivar ‘I-214’ was selected as the most suitable exotic poplar to plant for commercial plantations in Turkey (Birler 2014). Nevertheless, the scope of the study for selecting cultivar ‘I-214’ was limited to the observations conducted in the coastal regions of Turkey up to an altitude of 1000 m.a.s.l. In the following years, results from a countrywide study extended the scope of the observations and showed that the cultivar ‘I-214’ could be grown successfully in commercial plantations in Central, Eastern, and Southeastern Turkey where the continental and dry climatic conditions prevail. Since 2000, the cultivar ‘I-214’ and the *P. deltoides* cultivar ‘Samsun’ (synonym ‘I-77/51’) were successfully grown as commercial poplar plantations in the Marmara and Black Sea regions, while at the Coastal region, ‘Samsun’ may grow better than ‘I-214’ (Özel et al. 2010). It was observed that cultivar ‘Samsun’ was susceptible to unsuitable site conditions, particularly to drought. Therefore, plantations established with ‘Samsun’ are adversely affected by any negligence in plantation, maintenance operations, or irrigation failure (Birler 2014).

Turkey has been divided into two main zones according to climatic conditions: the Coastal or mild zone, which is suitable for *P.* × *euramericana* and *P. deltoides* cultivars, and the Continental zone, which is better for *P. nigra* cultivars (Velioğlu and Akgül 2016). This classification is based on the results of well-watered plantations and studies. However, there is a lack of research comparing the effects of drought on these cultivars. Since poplar requires abundant moisture to avoid water stress and maximize growth, and water availability in Turkey is seldom adequate for those requirements, species, hybrids, or cultivars that can withstand drought and grow well during water-limited periods need to be identified to maximize the productivity of *Populus* plantations. To sustain the extension of poplar cultivation from flood plains and bottomlands towards upland areas where seasonal drought are severe and irrigation is expensive or not possible to carry out, more drought-resistant cultivars are required to be identified.

Cytospora chrysosperma (Pers.) Fr. (the asexual state of *Valsa sordida* Nitschke) is one of the most important fungal diseases in Turkey. The bark necrosis, canker, and diebacks it produces on at least 85 host woody plant species (including poplar trees) are known worldwide (Sinclair et al. 1987; Uluer et al. 1998). The fungus is generally considered weakly parasitic entering through wounds that may be due to frost, sunscald, heat and drought stress, insect damage, or browsing damage by elk, deer, or domestic livestock. Several researchers have reported that drought-stressed plants are more susceptible to *Cytospora* cankers (Kepley and Jacobi 2000; McIntyre et al. 1996; Uluer et al. 1998). Even though a variation on resistance to this disease among some cultivars has been reported (Uluer et al. 1998; Aktaş and Şimşek 2010), not all the cultivars have been tested, especially under contrasting water availability conditions.

Selecting an appropriate cultivar plays a significant role in forest establishment, increase productivity on forest plantations, decrease pressure on natural forests, and mitigate climate change. Obtaining information about the most suitable genotype for sites with different water availability conditions is of paramount importance for the establishment of fast-growing plantations. Therefore, this study aims to (1) quantify the effects of water availability on morphology, growth performance, and disease susceptibility of 11 poplar cultivars registered or prominent with well growth performance in semi-arid regions in Turkey, and (2) to determine which cultivars can be proposed as better adapted for operational deployment on water-limited sites.

Materials and methods

Study site

The study was established at the Behiçbey poplar nursery in Ankara, Central Anatolia region of Turkey (39° 55′ 57″ N, 32° 45′ 03″ E; 823 m.a.s.l.) on March 2009. The soil is clay loam with no fertilizer addition and a pH of 8.1. The Central Anatolia region has a semi-arid continental climate with hot, dry summers and cold, snowy winters. Most of the region usually has low precipitation throughout the year. During 2010 and 2011, the site received an annual rainfall of 532 and 403 mm, respectively (Fig. 1). During July and August, the maximum daily temperature ranged between 28.2 and 39.0 °C during 2010

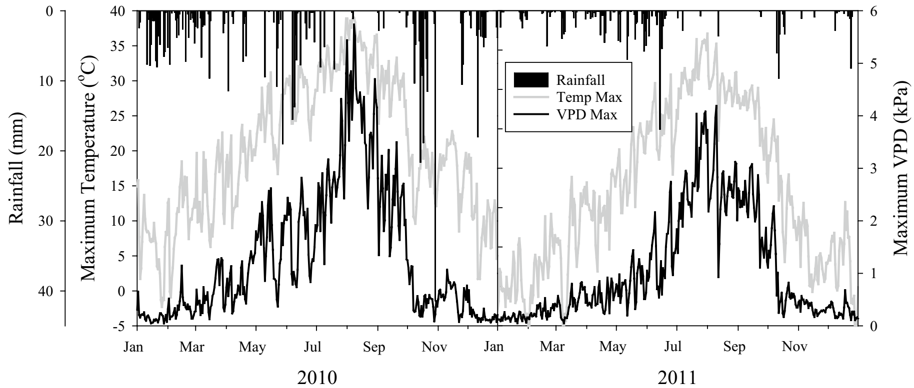

Fig. 1 Daily rainfall (vertical bars), maximum temperature (grey line) and maximum vapor pressure deficit (black line) for the study site

and between 23.5 and 37.1 °C during 2011. During the same period, the maximum daily vapor pressure deficit ranged between 1.2 and 5.7 kPa during 2010 and between 0.9 and 4.2 kPa during 2011. Weather data shown in Fig. 1 was obtained from a weather station of the Turkish Meteorological Service located at 5 km from the study site (Ankara-Etimesgut station).

Experimental design

The experiment consisted of testing 11 different cultivars of poplar in two watering treatments (well-watered, WW, and water-stressed, WS). To facilitate the application of the watering treatments, the study area was divided into two watering plots. Inside each watering plot, three blocks of eleven randomly-assigned cultivar sub-plots were established. During the first growing season (May to September 2009), both plots were irrigated by inundation every 2 weeks. During the second (May to October 2010) and third (May to October 2011) growing seasons, water stress on the WS plot was induced by irrigation cessation (irrigating only if the leaves wilted), while the WW plot was kept well-watered using weekly irrigation. The cultivars investigated were: *P. deltoides* cultivar 'Samsun'; *P. nigra* cultivars 'Anadolu', 'Ata-1', 'Behicbey', 'Cubuk-1', 'Cubuk-2', 'Gazi', 'Geyve', and 'Kocabey'; and *P.* × *euramericana* cultivars 'I-214' and 'I-45/51'. In March 2009, five 15 cm long unrooted cuttings of the 11 selected poplar cultivars were planted inside each cultivar sub-plot. Each cultivar sub-plot consisted of a single row of 5 trees planted at a spacing of 2.5 × 0.5 meters. A buffer row was planted surrounding each watering plot and a 2 m depth drainage channel was established between the watering plots to eliminate water draining from the WW to the WS plot. The experiment consisted of three replicates of each sub-plot in a randomized design, for a total of 330 trees (2 watering treatments × 3 replicates × 11 cultivars × 5 trees per sub-plot). In May 2009, a systematic pruning left only the longest shoot on each stool. Mechanical weed control was periodically applied to eliminate competing vegetation.

For both watering treatments, irrigation was carried out using inundation channels between planting rows. During the 2010 growing season, predawn leaf water potential (Ψ_{PD}, MPa) was measured bi-weekly on all plots using a pressure chamber (PMS Instruments Co., OR, USA). On both WW and WS plots, Ψ_{PD} was measured on one leaf from one randomly selected tree of each cultivar sub-plot. Data from all 11 cultivars were pooled to get one mean value per each watering treatment (Fig. 2). We used Ψ_{PD} as an indicator of the amount of water stress induced by the cessation treatment on trees growing at the WS plot and not to assess the water stress on each cultivar.

Growth and phenology measurements

Tree height (H, cm) and ground line diameter (D, cm) were measured every 3 weeks during the second growing season, for a total of 9 measurement times. At the end of this period, leaf loss percent was visually estimated for each tree as the proportion of the crown that fell during the autumn (compared to maximum leaf-out during the summer), at three different times (October 25, November 2 and November 30, 2010). During the third growing season, bud break phenology was assessed on April 26, May 2, and May 10, 2011, and was divided into three stages: 0, when buds were closed; 1, when buds just opened; and 2, when leaves were visible and unfolded. Additionally, damage by *C. chrysosperma* infection was assessed on May 10, 2011, using visual observations of disease signs and symptoms on

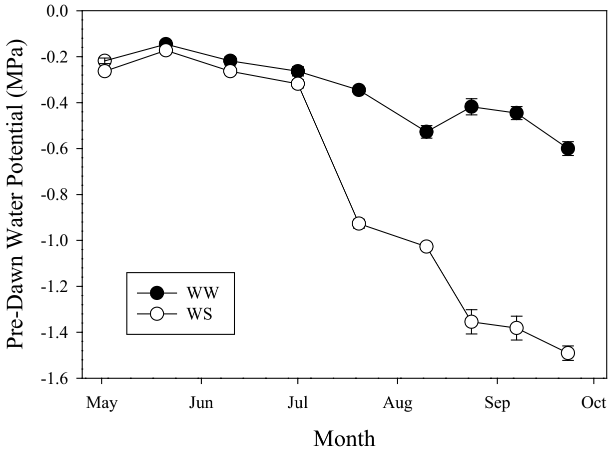

Fig. 2 Predawn leaf water potential during the second growing season (2010) of poplar cultivars growing under well-watered (WW, filled circle) and water-stressed (WS, open circle) conditions in Ankara, Turkey. Error bars represent standard error across all 11 cultivars (one sample per cultivar)

each tree (Aktaş and Şimşek 2010). The proportion of infected trees by treatment and cultivar was recorded. Observed dieback and canker signs and symptoms consisted of fruiting bodies as well as orange to reddish-brown spore masses. The cankers on the affected stems were either sunken, dark-colored lesions or cracks on the stem, formed as a result of dried bark that had separated from the underlying wood.

Determination of vegetation period

Each of the 11 cultivars had different starting and ending growing dates (i.e., a different vegetation period) which is a fundamental parameter to consider when comparing the growth performance of different genetic material, especially when grown under stress conditions, such as drought. Height (DOY H5) and diameter (DOY D5) growth starting date were determined as the value of the x-axis (day of the year, DOY) that corresponds to 5% more than the initial height (H5) or diameter (D5), respectively. Similarly, height (DOY H95) and diameter (DOY D95) growth ending date were determined as the value of the x-axis (DOY) that corresponds to 95% of the maximum height (H95) or diameter (D95), respectively. Height (H_{length}) and diameter (D_{length}) growth period length were computed as the number of days between H5 and H95, or D5 and D95, respectively. An example of vegetation period parameters is shown in Fig. 3.

Dates for starting and ending of height and diameter growth were determined by non-linear model fitting on mean values per sub-plot of height and diameter measured every 3 weeks. Model selection was carried out after comparing the coefficient of determination (R^2) and the Bayesian information criterion (BIC) for different sigmoidal functions tested. The model selected, a four-parameter logistic function, had the form

$$X = y_0 + \frac{a}{1 + e^{-(DOY - x_0)/b}}$$

where X is the growth parameter evaluated (D or H), DOY is the day of the year (of the Julian calendar) assigned to the corresponding measurement time, y_0 is the lower asymptote as DOY $\rightarrow -\infty$, a is the upper asymptote as DOY $\rightarrow \infty$, x_0 is the inflection point, and b is the scale parameter (Pinheiro and Bates 2000).

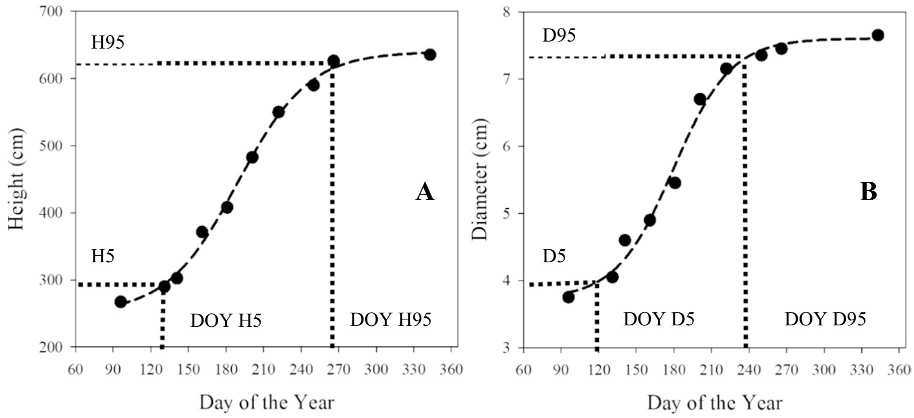

Fig. 3 Example of height (**a**) and ground line diameter (**b**) growth starting and ending dates. A sigmoidal curve was fit from data of each tree from each cultivar on each water availability treatment

Statistical analysis

Analysis of variance including Bonferroni adjustment was used to test the effects of treatments (cultivars x watering) on sub-plot means of seasonal growth (height and ground line diameter), vegetation period (DOY H5, DOY H95, DOY D5, DOY D95, H_{length}, and D_{length}), leaf loss percent, bud break stage and fungus infection damage (PROC GLM; SAS Institute Inc., Cary, NC, USA). Logit transformation was performed for leaf loss percent, bud break stage, and fungus infection damage.

Correlation analysis and non-linear model regression were used to test the relationships between leaf loss percent and H_{length}, leaf loss percent and fungus infection, fungus infection and height growth, bud break stage and fungus infection, and bud break stage and leaf loss percent (PROC GLM, PROC REG, and PROC NLIN). Model assumptions of normality, linearity, and constant variance were examined on the residuals of each variable (PROC UNIVARIATE). Where non-linear model fitting was carried out, an empirical R^2 (Myers 2000) was determined as:

$$R^2 = 1 - \frac{SSE/df_e}{SST/df_t}$$

where SSE and SST are the sum of squares of residuals and total, respectively, and df_e and df_t are the degrees of freedom of error and total, respectively. When the non-linear model fitting was carried out, several models were tested and the BIC was used for final model selection.

Results

Table 1 shows the *P* values for ANOVA for watering, cultivar, and the interaction of both treatments, for each trait evaluated. Water availability showed a non-significant effect only for H growth starting date (DOY H5). The interaction between water availability and

Table 1 Summary of ANOVA for growth and phenology traits for water × cultivar treatments

Trait	P > F		
	Water	Cultivar	Water × cultivar
DOY H5	0.424	**0.0003**	0.577
DOY D5	**< 0.0001**	0.142	0.955
DOY H95	**< 0.0001**	**0.003**	**< 0.0001**
DOY D95	**< 0.0001**	0.129	0.512
H_{inc}	**< 0.0001**	0.110	**0.013**
D_{inc}	**< 0.0001**	0.126	0.338
H_{length}	**< 0.0001**	0.117	0.0006
D_{length}	**< 0.0001**	0.276	0.721
LL_{102510}	**< 0.0001**	0.161	**0.0006**
LL_{110210}	**< 0.0001**	0.146	**0.0003**
LL_{113010}	**0.0006**	**0.0004**	**0.001**
$Fungi_{051011}$	**< 0.0001**	**0.001**	**0.001**
BB_{042611}	**< 0.0001**	**< 0.0001**	**0.0003**
BB_{050211}	**< 0.0001**	**0.036**	**0.036**

DOY H5, day of the year when height growth was 5% of the initial; DOY D5, day of the year when diameter growth was 5% of the initial; DOY H95, day of the year when height growth was 95% of the total growth; DOY D95, day of the year when diameter growth was 95% of the total growth; H_{inc}, height increment; D_{inc}, diameter increment; H_{length}, height growth period length; D_{length}, diameter growth period length; LL_{102510}, leaf loss % on October 25, 2010; LL_{110210}, leaf loss % on November 2, 2010; LL_{113010}, leaf loss % on November 30, 2010; $Fungi_{051011}$, infection by *C. chrysosperma* on May 10, 2011; BB_{042611}, bud break stage on April 26, 2011; BB_{050211}, bud break stage on May 2, 2011

P-value shown is in bold if the difference across treatments was significant at $\alpha = 0.05$

cultivar was non-significant for height growth starting date (DOY H5), and diameter (DOY D5, DOY D95, D_{inc}, and D_{length}).

Survival and height and diameter growth

Tree mortality at the end of the first growing season (October 2010) was null among the 11 cultivars (data not shown). There was a strong effect of water availability on height increment (final height − initial height, H_{inc}) (Table 1; $P < 0.0001$). All the cultivars doubled their height at the WW treatment (Fig. 4a). When growing under WW treatment, H_{inc} of cultivar 'Samsun' (Fig. 4a, filled black circle) was significantly larger than H_{inc} of cultivar 'I-45/51' (Fig. 4a, open grey triangle), and were the only two cultivars showing differences (3.16 m vs. 2.17 m, $P = 0.010$). There were no differences in H_{inc} among cultivars in the WS treatment (Fig. 4b, $P = 0.110$). There was a significant interaction (Table 1; $P = 0.013$) between the cultivars and watering treatments for H_{inc}, which means that some of the cultivars differed in their height growth between the watering treatments, while others did not. In our case, the cultivar 'I-45/51' (*P.* × *euramericana* cultivar) was the only one that was not affected by the watering regime, having a similar low growth response under both treatments.

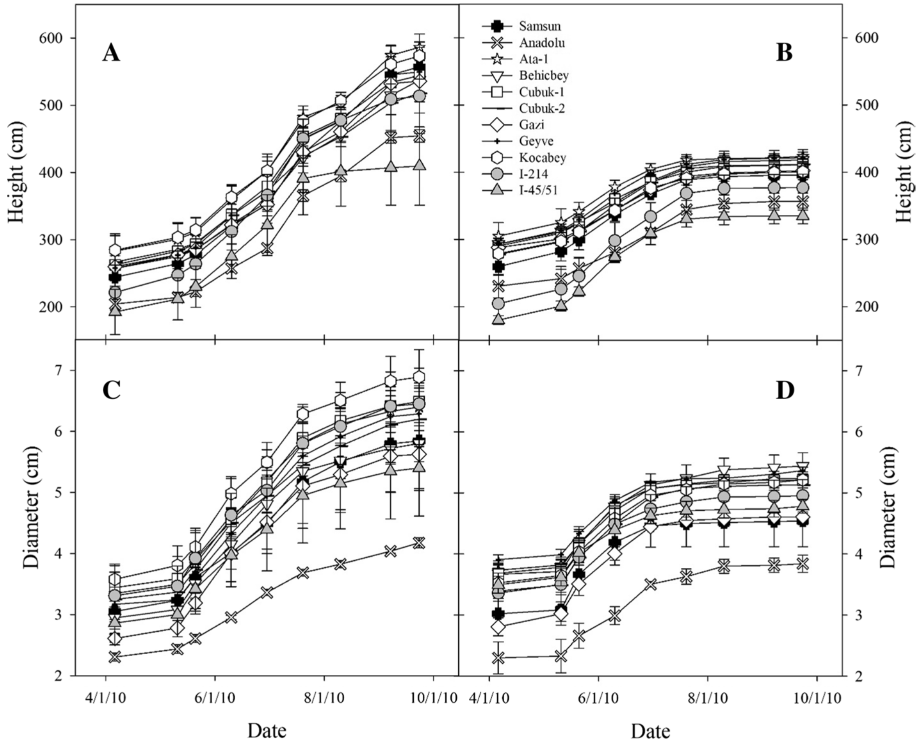

Fig. 4 Seasonal dynamics of height (**a**, **b**) and ground line diameter (**c**, **d**) for 11 poplar cultivars growing under well-watered (**a**, **c**) and water-stressed (**b**, **d**) conditions in Ankara, Turkey. Error bars represent standard error. Cultivars from *P. deltoides*, *P. nigra* and *P.* × *euramericana* are depicted with black, white, and grey, respectively. Note that at the beginning of the 2010 growing season, height and diameter were similar for both watering treatments

Diameter increment (final diameter − initial diameter, D_{inc}) of poplar cultivar trees was strongly affected by watering treatments (Table 1). WW poplar cultivars showed larger D_{inc} than WS trees ($P < 0.0001$), averaging D_{inc} of 3.0 cm during the first growing season (Fig. 4c), while in the WS treatment the average D_{inc} was 1.6 cm (Fig. 4d). Even though D_{inc} was different between both watering treatments, there were no differences in D_{inc} among cultivars ($P = 0.126$), meaning that the ranking of cultivar growth was approximately the same for both watering treatments. There was no significant interaction in D_{inc} among cultivars and water availability treatments ($P = 0.338$).

Vegetation period

Height growth starting date (DOY H5) was not affected by watering treatments (Table 1). DOY H5 occurred on May 4 and May 5, for the WW and the WS treatments, respectively (Fig. 5a; $P = 0.424$). However, cultivars showed different DOY H5 ($P = 0.0003$), with cultivars 'I-214' and 'I-45/51' having a DOY H5 of about 10 days earlier than cultivars 'Anadolu' and 'Gazi', across treatments. On the other hand, there was a significant interaction between cultivar and watering treatments on DOY H95 ($P < 0.001$) and H_{length} ($P = 0.0006$), which implies that height growth ending date

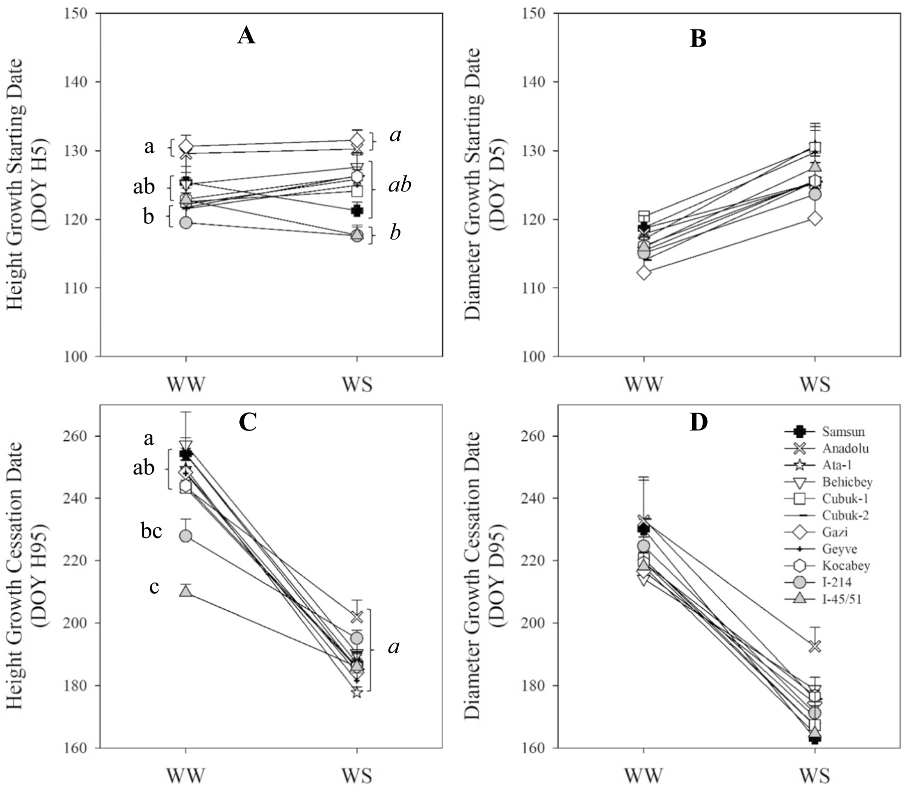

Fig. 5 Height (**a**, **c**) and ground line diameter (**b**, **d**) growth starting (**a**, **b**) and ending (**c**, **d**) dates for 11 poplar cultivars growing under well-watered (WW, left) and water-stressed (WS, right) conditions in Ankara, Turkey. Error bars represent standard error. Cultivars from *P. deltoides*, *P. nigra* and *P.* × *euramericana* are depicted with black, white, and grey, respectively. Letters represent statistical differences among cultivars within each watering treatment at $\alpha = 0.05$ (italic letters for the WS treatment). Letters are shown when cultivar and/or water x cultivar effects were significant

was different among cultivars and across watering treatments, affecting the length of the growing season for height (Figs. 5 and 6). In the WW treatment, DOY H95 of cultivar 'I-45/51' differed from all other cultivars ($P < 0.009$) except for cultivar 'I-214'. Besides, DOY H95 of 'I-214' only differed from cultivar 'Behicbey' ($P = 0.043$). Cultivars 'Ata-1' and 'I-45/51' ceased height growth on September 7 and July 29, respectively, when growing under WW conditions. However, DOY H95 was June 27 and July 5, respectively, when growing under WS. On average, the height growth ending date was 56 days earlier for trees growing in the WS treatment (Fig. 5c).

Similar to D_{inc}, diameter vegetation period parameters (DOY D5, DOY D95, and D_{length}) were strongly affected by watering treatments (Table 1; $P < 0.0001$). DOY D5 was on average 10 days later for cultivars growing in the WS treatment (Fig. 5b; $P < 0.0001$). Neither cultivars ($P = 0.142$) nor watering × cultivar interaction ($P = 0.955$) have an effect on DOY D5. Diameter growth ending date (DOY D95) was on average 50 days earlier for the cultivars in the WS treatment compared to the WW (Fig. 5c; $P < 0.0001$). Diameter growth period length (D_{length}) was on average 60 days shorter for

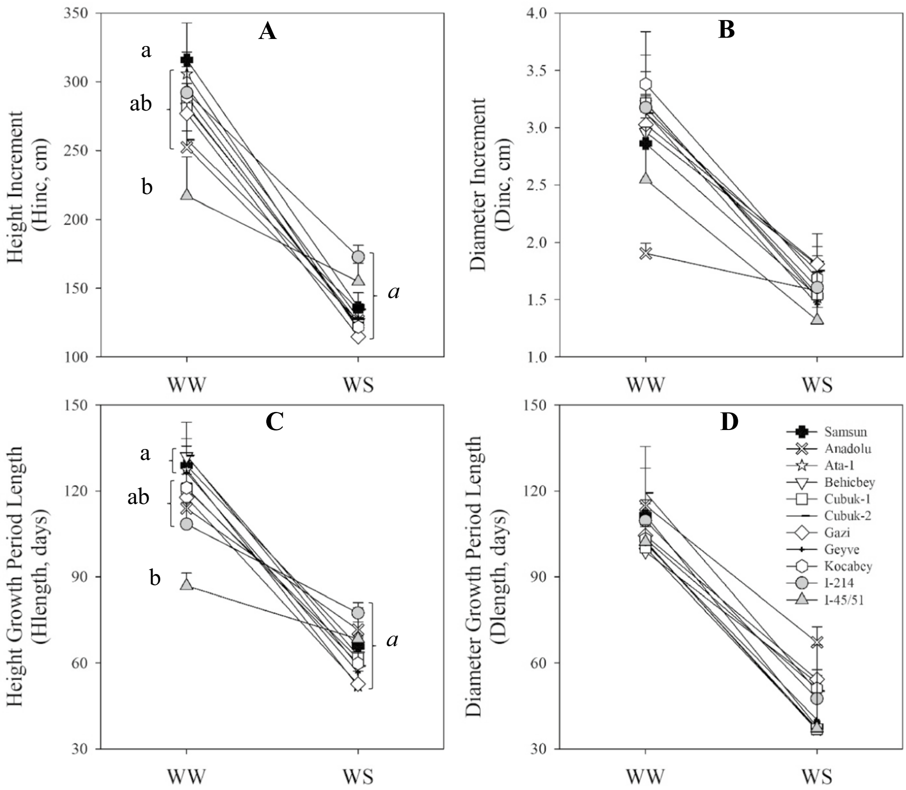

Fig. 6 Height (**a**, **c**) and ground line diameter (**b**, **d**) increment (**a**, **b**) and growth period length (**c**, **d**) for 11 poplar cultivars growing under well-watered (WW, left) and water-stressed (WS, right) conditions in Ankara, Turkey. Error bars represent standard error. Cultivars from *P. deltoides*, *P. nigra* and *P.* × *euramericana* are depicted with black, white, and grey, respectively. Letters represent statistical differences among cultivars within each watering treatment at $\alpha = 0.05$ (italic letters for the WS treatment). Letters are shown when cultivar and/or water x cultivar effects were significant

the cultivars in the WS treatment compared to the WW ($P < 0.0001$). Neither cultivar nor watering × cultivar interaction affect DOY D95 or D_{length} (Figs. 5 and 6).

Leaf loss

There was a significant interaction between cultivar leaf loss across watering treatments ($P = 0.0006$, 0.0003, and 0.001, for measurements carried out on October 25, November 2, and November 30, respectively). Leaf loss percent of poplar cultivars during early autumn (October 25, 2010) was strongly affected by watering treatments (Table 1). For the WW treatment leaf loss percent averaged 12.8%, while in the WS treatment it was 67.2% (Fig. 7a). On November 30, 2010 (Fig. 7b), in the WW treatment, cultivar 'Cubuk-2' had the least leaf loss (60.7%), and it was different from cultivars 'Samsun', 'I-214', and 'I-45/51' ($P < 0.039$) that lost 100% of their leaves. The significant watering by cultivar interaction implies that cultivars responded differently and changed their ranking between the watering treatments. For example, cultivars 'I-214' and 'Geyve' had a 100% and 65%

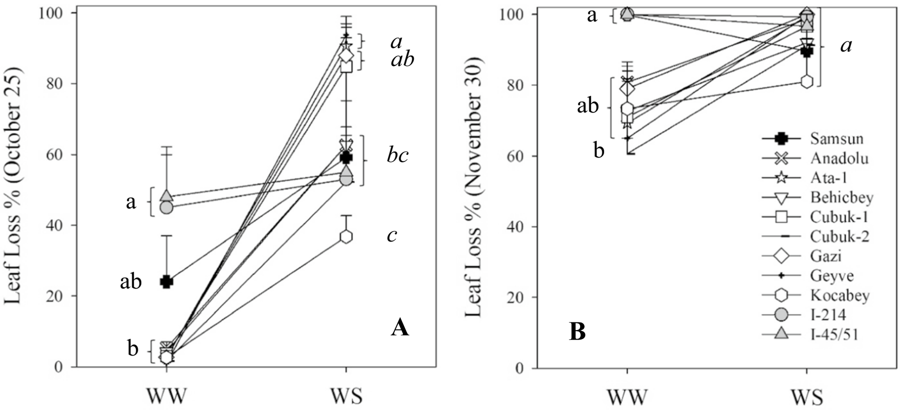

Fig. 7 Leaf loss percent during two dates in autumn 2010, October 25 (**a**) and November 30 (**b**) for 11 poplar cultivars growing under well-watered (WW, left) and water-stressed (WS, right) conditions in Ankara, Turkey. Error bars represent standard error. Cultivars from *P. deltoides*, *P. nigra* and *P.* × *euramericana* are depicted with black, white, and grey, respectively. Letters represent statistical differences among cultivars within each watering treatment at α = 0.05 (italic letters for the WS treatment). Letters are shown when cultivar and/or water x cultivar effects were significant

of leaf loss, respectively, when growing in WW plots. However, when growing under WS conditions, both cultivars showed 100% and 99.7% of leaf loss, respectively.

Cultivar leaf loss as a response to water availability differed for each evaluation date. For example, cultivar 'Samsun' showed greater leaf loss when growing under the WS treatment on October 25 and less on November 30. On the other hand, the cultivar 'I-214' presented a less marked leaf loss than cultivar 'Samsun' on October 25 and practically the same defoliation in both treatments on November 30.

Cytospora chrysosperma infection

In addition to the strong effect of water stress on susceptibility to *C. chrysosperma* (all poplar cultivar trees growing under WW conditions showed no signs of fungus infection), there was a strong interaction between cultivar and watering treatments (Table 1; $P = 0.0001$). During the 2011 growing season, in the WS treatment, about 7% of the trees from cultivars 'Samsun', 'I-214', and 'Kocabey' were infected by *C. chrysosperma*, and only cultivar 'I-45/51' was completely resistant to the disease (Fig. 8). Nonetheless, 'Samsun', 'I-214', 'Kocabey', and 'I-45/51' were only different from cultivars 'Ata-1', 'Gazi', and 'Geyve' ($P < 0.001$) that had nearly 80% of infection.

Bud break stage

Bud break was assessed during the third growing season (2011) and occurred earlier in the WW treatment. The bud break response on April 26 (Fig. 9a) showed a significant interaction between watering and cultivar treatments (Table 1, $P = 0.0003$), implying that some cultivars responded differently under varying water availability conditions. In the WW treatment, exotic poplar cultivars 'Samsun' (*P. deltoides*), 'I-214', and 'I-45/51'

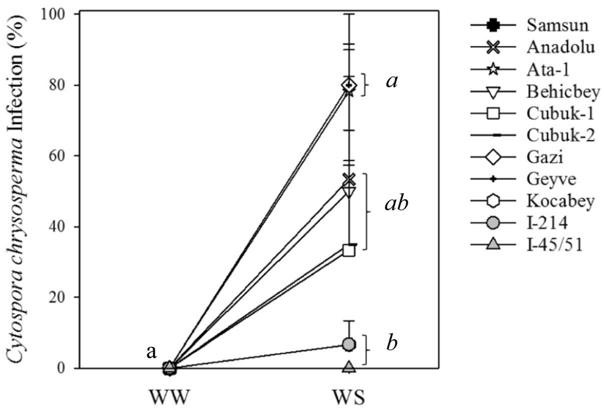

Fig. 8 Infection by *Cytospora chrysosperma* during the 2011 growing season (May 10) for 11 poplar cultivars growing under well-watered (WW, left) and water-stressed (WS, right) conditions in Ankara, Turkey. Error bars represent standard error. Cultivars from *P. deltoides*, *P. nigra* and *P.* × *euramericana* are depicted with black, white, and grey, respectively. Letters represent statistical differences among cultivars within each watering treatment at α = 0.05 (italic letters for the WS treatment). Letters are shown when cultivar and/or water × cultivar effects were significant

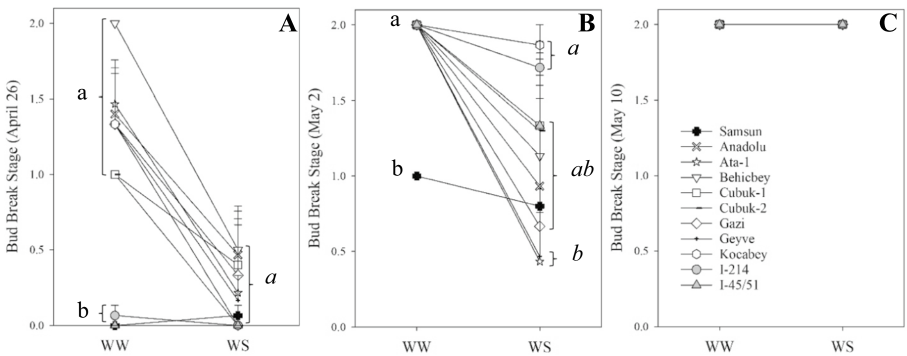

Fig. 9 Bud break stage (0 = bud is closed; 1 = bud braked; 2 = leaf is visible and unfolded) during three dates in spring 2011, April 26 (**a**), May 2 (**b**) and May 10 (**c**) for 11 poplar cultivars growing under well-watered (WW, left) and water-stressed (WS, right) conditions in Ankara, Turkey. Error bars represent standard error. Cultivars from *P. deltoides*, *P. nigra* and *P.* × *euramericana* are depicted with black, white, and grey, respectively. Letters represent statistical differences among cultivars within each watering treatment at α = 0.05 (italic letters for the WS treatment). Letters are shown when cultivar and/or water x cultivar effects were significant

(*P.* × *euramericana*) were different from all black poplar cultivars ($P < 0.002$). When growing in the WS treatment, all cultivars showed no differences in the bud break stage.

On May 2, the bud break stage still showed a significant interaction between watering treatment and cultivar (Table 1, $P < 0.036$). All the cultivars in the WW treatment had visible and unfolded leaves, except for cultivar 'Samsun', which was significantly different (Fig. 9b, $P = 0.002$). However, in the WS treatment, the cultivars ranged between starting to break buds to unfolded leaves. For example, cultivars 'Ata-1' and 'Geyve' were classified as having a bud break between 0.4 and 0.5 (opening buds), while cultivars 'I-214' and ‘Kocabey’ were classified between 1.7 and 1.9 (leaves almost unfolded). On May 10 (Fig. 9c), all the cultivars at both watering treatments had visible and unfolded leaves.

Relationships among the analyzed variables

Relationships among the analyzed variables were drawn to facilitate the visualization of the trade-offs and synergetic associations between commonly observed traits for poplar cultivars growing under semiarid conditions in Turkey.

Leaf loss percent observed on October 25, 2010, and height growth period length (H_{length}) were negatively correlated following a sigmoidal shape (Fig. 10a; $R^2 = 0.85$, $P < 0.001$), and this response was mainly driven by the effect of water availability. On the other hand, leaf loss observed on October 25, 2010, has a positive relationship (Fig. 10b; $R^2 = 0.81$, $P < 0.001$) with *C. chrysosperma* infection observed on May 10, 2011, meaning that the more water-stressed the trees were, the more leaf loss was observed, and the more infected by the fungi the trees were in the following season.

Poplar cultivars that showed no leaf loss during late October 2010 (well-watered) showed a H_{length} of about 130 days. On average, H_{length} was longer (between 110 and 130 days) when poplar cultivars showed leaf loss percent lower than 30%. After that point, H_{length} was highly reduced, reaching values of about 60 days when leaf loss was 60%. Even though leaf loss larger than 80% was observed on four cultivars of *P. nigra* (‘Ata-1’, ‘Çubuk-1’, ‘Çubuk-2’, and ‘Gazi’) growing under WS conditions, no further reduction in H_{length} was observed. Interestingly, cultivar ‘Kocabey’ growing under WS conditions showed reduced leaf loss (about 35%, comparable with some well-watered cultivars) but also showed H_{length} of about 60 days.

For trees growing in the WS treatment, *C. chrysosperma* infection (%) was negatively related ($R^2 = 0.62$, $P < 0.001$) to bud break stage (both observed in May of the 2011 growing season), meaning that the more infected by the fungi the trees were, the less open the buds were (Fig. 11a). The R^2 for the correlation goes up to 0.97 when excluding the cultivars ‘Samsun’ and ‘I-45/51’, whose resistance to *C. chrysosperma* infection did not guarantee an earlier bud break. The leaf loss observed on October 25, 2010, for trees growing in the WS treatment was negatively related ($R^2 = 0.64$, $P < 0.001$) to the bud break stage in the next growing season (May 2, 2011). Therefore, the less leaf loss experienced by the trees, the more open the buds were during the growing season immediately after (Fig. 11b).

Even though there was a negative correlation between defoliation (leaf loss) and height growth period length (H_{length}), some cultivars showed different response patterns for these traits (Fig. 10a). For example, cultivar ‘Kocabey’ showed the lowest leaf loss (37%) in the WS treatment, but shorter height growth period length ($H_{length} = 60$ days). On the other hand, for the same watering treatment, cultivar ‘I-214’ showed the longest height growth period length ($H_{length} = 77$ days) and a relatively low leaf loss (53%). In the WS treatment, the cultivar ‘Cubuk-1’ showed a high leaf loss (85%) although it showed a relatively low infection by *C. chrysosperma* (33%), indicating that it might not be suitable for semiarid conditions. However, cultivar ‘Kocabey’ has the lowest leaf loss (37%) and *C. chrysosperma* infection (7%) combined, indicating that it might be better suited for semiarid conditions.

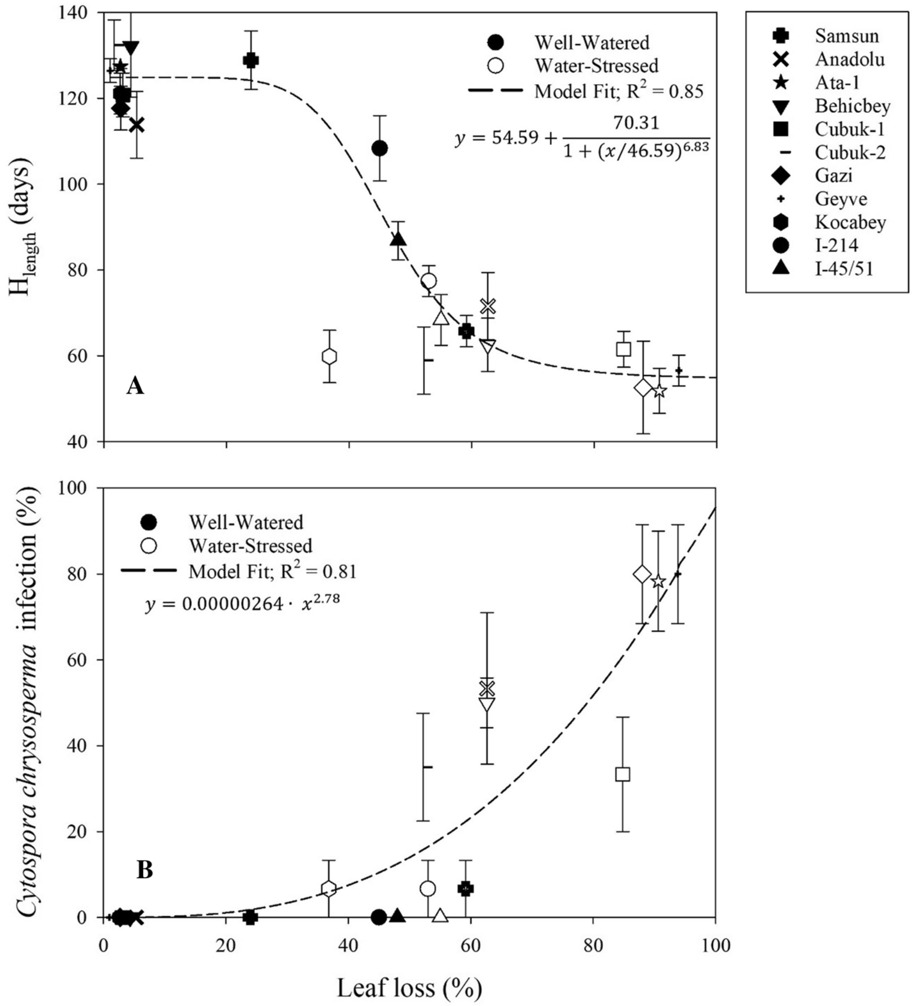

Fig. 10 Relationship between leaf loss (%) on October 25, 2010, and (**a**) height growth period length (H_{length}), and (**b**) *Cytospora chrysosperma* infection (%) on May 10, 2011, for the 11 poplar cultivars in the water-stressed (open symbol) and the well-watered (filled symbol) treatments. Error bars represent standard error. The dashed line represents the regressions fitted

Discussion

To survive under water-stressed conditions, plants typically possess morphological and physiological adaptations allowing sustained uptake and reduced loss of water (Baquedano et al. 2008; Nahar et al. 2015). Even though poplars are, in general, not considered drought tolerant (Rhodenbaugh and Pallardy 1993; Tschaplinski et al. 1998), all poplar cultivars assessed in this study survived under the water-limited conditions created in the WS treatment. Nevertheless, the level of water stress observed (Fig. 2) was below the thresholds associated with irreversible cavitation for these species (Fichot et al. 2015).

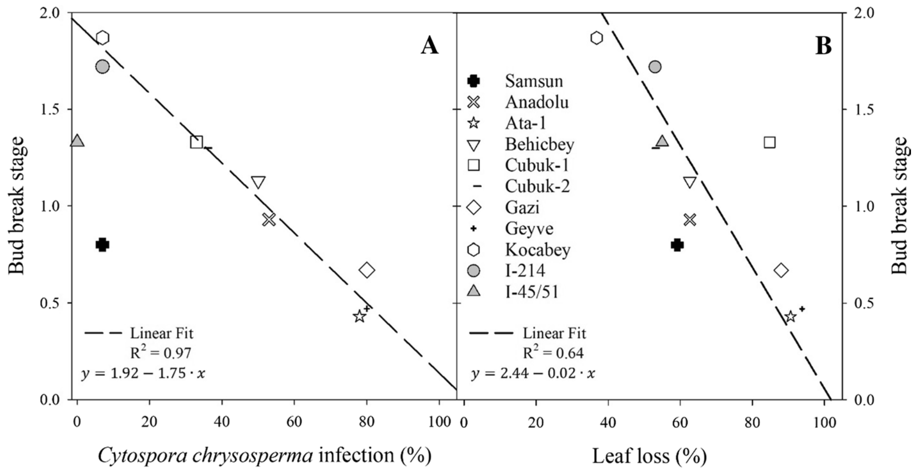

Fig. 11 Relationship between bud break stage on May 2, 2011, and (**a**) *Cytospora chrysosperma* infection (%) on May 10, 2011, and (**b**) leaf loss (%) on October 25, 2010, for the 11 poplar cultivars in the water-stressed treatment. The dashed lines represent the linear regressions fitted. Cultivars from *P. deltoides*, *P. nigra* and *P. × euramericana* are depicted with black, white, and grey, respectively

In this study, we found that water stress caused a significant reduction in height and diameter growth (Table 1). This is consistent with other studies that reported reduced growth of poplar trees under water stress compared to those growing with non-limited soil moisture (Mazzoleni and Dickman 1988; Rhodenbaugh and Pallardy 1993; Tschaplinski et al. 1998; Zhang et al. 2004; Yin et al. 2005; Monclus et al. 2006). Previous studies have suggested that there are cultivar variations in drought resistance within *Populus* species and hybrids (Pallardy and Kozlowski 1981; Strong and Hansen 1991; Tschaplinski and Tuskan 1994; Tschaplinski et al. 1994, 1998; Brignolas et al. 2000; Isık and Toplu 2004). Similarly, in this study, considerable differences were found among cultivars.

Several observed traits, such as height growth ending date (and therefore growth period length and total height growth), the timing of bud break, leaf loss, and infection by *C. chrysosperma* showed a strong interaction between genetics (cultivars) and environment (soil water availability), implying that cultivars responded differently and changed their ranking between the watering treatments. This differential response of the cultivars points towards differential selection under diverse soil water availability conditions.

Since 1965, black poplar cultivars such as 'Anadolu', 'Behicbey', 'Gazi', 'Geyve', and 'Kocabey' have been extensively planted in Turkey where the continental climatic conditions prevail, such as the semiarid climate of the study site in Ankara (Velioglu and Akgül 2016). All those cultivars showed superior growth under well-watered conditions, outperforming *P. × euramericana* cultivars ('I-214' and 'I-45/51'). Nevertheless, when growing under reduced soil water availability conditions, the cultivar 'Gazi' showed reduced growth, comparable with both *P. × euramericana* cultivars. These results have important management implications, as this cultivar has been largely planted in Eastern regions of Turkey (Tunçtaner and Özel 2008), and the productivity of this cultivar may be highly affected under increasing drought conditions.

Height growth starting date, which on average was between May 4 and 5, was not affected by watering treatments. This response indicates that height growth initiation is controlled mainly by radiation and temperature rather than plant water status (Kramer and Kozlowski 1960; Rohde et al. 2011; Bussotti et al. 2015). It is important to consider that irrigation treatments started at about the same time and soil moisture (reflected in pre-dawn water potential) was similar across watering treatments by that time. Nevertheless, *P.* × *euramericana* cultivars showed an earlier starting date of about 10 days, indicating that these cultivars, that evolved in regions with a milder climate than the study site (Stanton et al. 2014; Velioğlu and Akgül 2016), can take advantage of initiating height growth sooner when exposed to higher temperatures.

On the other hand, the height growth ending date showed a strong genetic x environment interaction. When growing under well-watered conditions, cultivars from *P.* × *euramericana* showed earlier ending dates than the other cultivars, however, when growing under water-stressed conditions, there were no differences among cultivars. The reduced sensitivity of height growth ending date to reduced water availability of *P.* × *euramericana* indicates that these cultivars can take little advantage of growing under elevated soil water availability. Our results showed that, in addition to photoperiod and temperature that has been reported by others (Howe et al. 2003; Rohde et al. 2011), plant water status can play a key role in height growth dynamics of poplars.

Starting and ending dates of diameter growth were not different among cultivars, but were highly affected by watering treatments. This lack of genetic control and high environmental control on diameter phenology has important management implications, as poplar cultivars deployed on sites with similar soil water availability will show similar diameter phenology among them.

Regardless of their height and diameter growth, cultivars 'I-214' and 'Kocabey' may be more suitable for semiarid conditions as they did not experience a severe leaf loss during the second growing season and their buds opened earlier the year immediately after. In the water-stressed treatment, the cultivar 'I-214' had the tallest height growth (173 cm) followed by the cultivar 'I-45/51' (155 cm). Cultivar 'Kocabey' and both *P.* × *euramericana* cultivars are resistant to *C. chrysosperma* infection, ranging from 0 to 7% of infection. Similarly, Uluer et al. (1998) indicated that cultivar 'I-214', together with 'Anadolu', were more resistant to *C. chrysosperma* infection (the authors tested fungus inoculation under well-watered conditions). Although these cultivars can grow more when no water stress is experienced, they reached 59% and 71% of their maximum height when growing with limited soil moisture availability. The other nine cultivars only grew 39–52% of their potential height when growing under water stress. Under water-limited conditions, cultivars 'Ata-1', 'Geyve', and 'Gazi' showed both, retarded bud opening and high susceptibility to *C. chrysosperma*, suggesting that they might not be suitable for semiarid conditions.

The timing of bud break (height growth initialization) and leaf loss are determined to a large extent by changes in tree water status (Reich and Borchert 1984), but this response is controlled by the interactive effect of the water status of the environment (soil and air) and the physiology of the trees (Lloret et al. 2018). In our study, well-watered trees showed earlier bud break and cultivars of black poplar showed earlier bud break than *P. deltoides* and *P.* × *euramericana* cultivars. Even when growing under well-watered conditions, black poplar cultivars showed a large degree of variation of bud break stage. While cultivars 'Cubuk-1' and 'Cubuk-2' showed a broken bud, cultivar 'Behicbey' showed unfolded leaves on April 26, 2011. This response can prevent the establishment of 'Behicbey' cultivar in some areas prone to late-spring freeze events, as delayed bud break play an important role in avoiding potential late-spring frost damage (Bussotti et al. 2015; Deacon et al. 2019).

Conclusions

This study provides valuable information to better understand the interactive effects of reduced soil moisture availability on growth and phenology of 11 poplar cultivars. Our conclusions are based on observations performed using a selection of widely planted poplar cultivars in Turkey. Even though other cultivars are available to date, the genotypes used in this study still represent the most important cultivars for commercial purposes in Turkey (Birler 2014; Velioğlu and Akgül 2016). Although we performed our evaluations during the first three growing seasons after planting, our results can help to select the cultivars that would perform better under semiarid conditions in Turkey. Cultivars 'I-214' and 'Kocabey' may be adequate alternatives for planting under water-limited sites. Conversely, planting cultivars 'Ata-1', 'Gazi', and 'Geyve' may not be preferred under the aforementioned conditions. Our results may imply extending the area for establishing poplars, by including water-limited sites that are currently considered unsuitable for productive plantations, and decreasing operational costs due to reduced irrigation intensity. Further research is needed to assess long-term responses in drought resistance and productivity, as well as the effects of successive drought events in the physiology and performance of poplar cultivars.

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