



Time-course foliar dynamics of poplar short rotation plantations under Mediterranean conditions. Responses to different water scenarios

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ABSTRACT

Poplar (*Populus* spp.) Short Rotation Coppice (SRC) systems are characterized by high short-term biomass productivity and play a key role in promoting employment in rural areas as well as supplying environmental benefits. However, in the context of climate change with expected reduced water availability in the Mediterranean area, the productivity of these plantations may be seriously limited. In this regard, the aim of this work is to analyse the monthly dynamic responses of relevant variables at foliar level throughout the entire first rotation of a poplar short rotation plantation under two water scenarios: optimal scenario (with irrigation to field capacity (FC)) versus restrictive scenario (with 50% FC irrigation).

This data came from 590 trees in a poplar short rotation plantation of the highly productive genotype 'AF2'. LAI_{max} values of 2.39, 7.47 and 9.34 were found for the three-year rotation cycle, pointing to significantly lower values after the establishment year under the restrictive water scenario. SLA mean values displayed a downward trend, with 12.25 m² kg⁻¹, 10.82 m² kg⁻¹ and 10.47 m² kg⁻¹ for years 1, 2 and 3 respectively, no significant differences being observed between water scenarios. NPK foliar concentrations decreased over the rotation, being the values lower under the restrictive scenario. Additionally, the selected genotype, 'AF2', displayed tight stomatal control under conditions of water stress, maintaining high photosynthetic levels.

The responses observed in this study can potentially be used to better understand the behavior of these variables which most affect production of poplar plantations in face of climate change.

1. Introduction

The transition to an advanced bio-based economy is a key element to ensure smart green growth in Europe [1]. There is much expectation that biomass plantations will play a key role in the context of promoting the bioeconomy strategy. Commercial plantations of Poplar (*Populus* spp.) grown under Short Rotation Coppice (SRC) systems provide a source of raw material for bioenergy and/or bioproducts, promoting employment in rural areas as well as supplying environmental benefits [2,3]. Furthermore, these plantations make an important contribution towards reaching a low carbon bioeconomy [4,5].

Hybrid poplars under this management system are characterized by their high productivity over a short time period. Moreover, they are managed in a sustainable way [6] without competing with biomass resources from forests [7]. However, productivity may be seriously limited

by water deficit during the growing season [8]. Irrigation is an indispensable operation not only to ensure their survival under Mediterranean conditions [9] but also to achieve high productivity in other areas of Europe [10–12] and around the world [13,14].

In order to optimize the management of these systems to maximise biomass production and meet the demands of the market as well as to develop more accurate predictive management tools, it is crucial to understand tree allometry and growth. In recent years, considerable progress has been made in this regard [15], especially in the development of specific predictive models for SRC plantations under Mediterranean conditions [16–18]. However, more reliable predictive models based on ecophysiological processes could further contribute to our understanding of crop development and therefore help to promote this type of plantation. The precision of the model estimates would be improved by taking into account changes in allometry and physiology as

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a result of limited water availability, not only in Mediterranean environments but also in other areas where reduced water availability is likely in the foreseeable future. These enhanced models would also enable us to simulate different climate change scenarios under which limited water availability will increasingly become a reality. Hence, it is necessary to further our understanding of the behavior of each fraction and the role they play in the growth of the tree. The foliage fraction is an essential component in this regard, because it constitutes the primary interface between the trees and their atmospheric environment, therefore being key to the ecophysiological relationships [19].

Poplar foliage biomass and therefore the Leaf Area Index (LAI) is never static. It changes continuously, producing the full complement of leaves each season [19]. These changes are even more pronounced in short rotation crops, where frequent cuttings occur, usually every 3 years [20]. There is a strong correlation between biomass production and LAI over time [21,22], this correlation being very high ($r^2 = 0.96$) at least until LAI reaches values of 6 [23]. In this regard, Scarascia-Mugnozza et al. [24] showed that the clonal ranking of biomass production and the LAI was highly coincident. The limitations on plant production caused by water stress can affect foliar traits at morphological, physiological and biochemical scales [25–27]. Monclus et al. [28,29] studied 33 poplar genotypes under water deficit conditions and found significant reductions in foliar biomass as well as a decrease in maximal individual leaf area and SLA in response to drought.

Another parameter of special interest in the leaf fraction is the leaf nutrient content given the important role it plays in physiological processes such as photosynthesis, the plant-water relationship [30,31] and nutrient recirculation via leaf turnover. Identifying the concentrations of elements in plant tissues in terms of macro and micronutrients is highly important in order to optimize crop production and evaluate fertilizer requirements [32]. According to the literature the optimal range of NPK for *Populus* species is 17–30 g kg⁻¹ for N, 1–4.4 g kg⁻¹ for P and 7–20 g kg⁻¹ for K [33]. Inadequate supply of any nutrient will affect canopy photosynthesis and in turn the biomass production [19]. Identifying nutrient dynamics is essential to understanding and predicting the effects of nutrition on tree growth [19]. C and NPK stoichiometry provides a powerful indicator of diverse ecological and physiological processes, revealing evident responses to environmental condition such as water stress during growth [34].

Gas exchange measurements can also provide important indications of water stress at leaf level. Stomatal conductance (g_s) for instance is used to characterize the plant water status because of its relationship with stomatal behavior and osmotic adjustments [35]. The relationship between the photosynthesis rate and the transpiration or stomatal conductance provides an instantaneous estimate at leaf level of the water use efficiency (WUE) or the intrinsic water use efficiency (IWUE), respectively, more or less dependent on the environmental factors [36]. Furthermore, at biochemical level, parameters such as soluble sugar content, proline levels, malondialdehyde (MDA) and in general the activity of antioxidant enzymes are affected by water restrictions [37].

Our research provides information on the monthly evolution of relevant variables at foliar level throughout the entire first rotation of a poplar short rotation plantation under different water scenarios. The aim of this study is to contribute towards more reliable predictions by process-based models in which specific parameterization of water deficit scenarios may be of interest. Monthly estimates could also be produced by considering specific leaf dynamics. A greater understanding of the behavior of these variables under conditions of limited water availability by analysing the monthly patterns may also be of particular interest, not only for modeling purposes, but also to identify the variables which most affect production, thus contributing to the development of improved breeding programs.

In summary, the aim of this research is to further our knowledge of foliar dynamics during the entire first rotation of a SRC plantation in which optimal irrigation was applied under a scenario of restricted water availability, focusing on:

- i) analysing the monthly foliage biomass production and distribution
- ii) comparing the monthly progression of Leaf Area Index (LAI) and Specific Leaf Area (SLA)
- iii) evaluating monthly nutrients - C, N, P and K leaf content, the Nitrogen Use Efficiency (NUE), and the Photosynthetic Nitrogen Use Efficiency (PNUE)
- iv) evaluating the most important ecophysiological variables - stomatal conductance (g_s), photosynthetic assimilation rate (A), transpiration rate (E), Water Use Efficiency (WUE), and the Intrinsic Water Use Efficiency (IWUE).

It is important to emphasize that this study isolates the effect of the genotype, which presents a pure signal that changes over the growing seasons. The poplar clone used in the experiment was 'AF2', selected specifically for biomass production [38].

2. Material and methods

2.1. Data source

Data for this work was collected from a poplar SRC plantation established in early spring 2018 for a rotation length of three years and a planting density of 10,000 trees ha⁻¹ (spacing 2 m × 0.5 m). The study site was located in central Spain (40° 27' 27" N; 3° 45' 01" W) at an elevation of 592 m a.s.l. The annual mean temperature was 14.66 °C, the annual mean precipitation was 425.5 mm and the soil has a sandy loam texture with a pH of 8.59.

The genotype used was 'AF2' (*Populus × canadensis* Mönch), which is widely used for the production of chip biomass in the Mediterranean area [38–40] and was specifically selected as a high biomass productivity clone for biomass production by the private forest nursery company Alasia Franco Vivai (Savigliano, Italy). The plantation was established manually using hardwood cuttings of 25 cm in length. Two different watering scenarios were applied (T1 and T2). The experimental plantation T1 was irrigated to field capacity (FC) and the adjoining plantation T2 consisted of half that dose (50% of FC). A drip irrigation system was used during the growing seasons (from May to October every year). Moisture in both trials was monitored using moisture sensors (SM200 Delta-T). A weed control fabric was spread over the whole area in order to avoid weed competition. Fertilization was not applied.

A total of 590 trees were planted. Each scenario (T1 and T2) consisted of five single rows with a total of 295 trees per water scenario, including inner and outer border rows to minimize these effects. Every month, on the 21st ± 3 days, during the 3 growing seasons of the rotation cycle (from April to November), 3 trees (sampling group) per scenario were harvested and inventoried, being in summary 6 harvested trees per month considering both water scenarios (T1 and T2). The data set is collected from 138 measured trees out of 590 at the end of the first rotation (no sample in April in the first year). The border effect within the sampling rows was also taken into account, establishing border trees between each sampling group.

Given the notable intra-annual variability with regard to the entire foliar phenology, only the months with active tree growth (June–September) were considered for comparison of some variables. This period is defined as the mid-growing season. Hence, although all the months of the growing seasons are shown, henceforth the mean values for each year and scenario refer to the mid-growing season.

2.2. Foliage fraction measurements

To monitor monthly changes in the foliage fraction in plantations T1 and T2 for all the years of the rotation, all leaves were measured for all destructively sampled trees. We counted all the leaves, per water scenario, from the bottom to the top of all stools and separated them into two categories, branch leaves and stools leaves, obtaining the total

amount of different leaves at stool and branch level per harvested tree. All collected leaves per category were then dried at 60 °C in a forced air oven to constant dry mass and weighed using a balance (EU-C 7500PQ) with an accuracy of 0.1 g to calculate the total dry foliar biomass per tree W_f (kg tree⁻¹).

2.3. Leaf area estimation

Each month from May to November during the first growing season, all the leaves present per sampling group (three trees) and scenario (T1 and T2) were fresh scanned in order to determine the leaf area per tree.

As leaf area determination by scanning all leaves on a tree was expected to be far more complex in the second and third years due to tree size, the required sample size to achieve a target sampling error of 5% was estimated for the second and third year by using the data from the first year as a reference. The simple random sampling estimators [41] were used to estimate sample size by considering the population variance observed in the first year as proxy of same parameter for the second and third years. A total of 2390 leaves were fresh scanned during the first year to calculate their individual green leaf area, in cm², using the ImageJ software [42]. The leaves were then dried at 60 °C in a forced air oven to constant dry mass to obtain their individual dry weight using a balance (EU-C 7500PQ) with an accuracy of 0.1 g. Different sample sizes of randomly collected leaves were compared in order to achieve this target. Finally, a subsample of 50 random leaves (ss_{50}) per tree was determined to be the minimum sample size, assuming a standard error of 4.33% in leaf area prediction.

2.4. Specific Leaf Area (SLA) and Leaf Area Index (LAI)

The total leaf area measured for the design-based sampling of 50 random leaves per tree linked to its dry mass is the Specific Leaf Area, SLA (m² kg⁻¹), according to Eq. (1).

$$SLA = \frac{Leaf\ area_{ss50}}{W_{fss50}} \quad (1)$$

where SLA is the Specific Leaf Area (m² kg⁻¹), Leaf area_{ss50} is the leaf area of the sub-sample of 50 leaves per tree (m² tree⁻¹) and W_{fss50} is the dry leaf biomass of the sub-sample per tree (kg tree⁻¹).

The total LAI was defined as the leaf area per unit ground surface area, following Eq. (2).

$$LAI = \frac{SLA \times W_f}{ground\ area} \quad (2)$$

where LAI is the Leaf Area Index (m² m⁻²), SLA is the Specific Leaf Area (m² kg⁻¹), W_f is the total dry leaf biomass per tree (kg tree⁻¹) and the ground area (m).

The Maximum Leaf Area (LAI_{max}) was calculated with the highest monthly mean LAI value for each growing season.

The individual mean leaf area was calculated as the mean value of leaf area per leaf.

2.5. Leaf nutrient analysis

To evaluate monthly C, N, P and K leaf nutrient concentrations, a sub-sample was randomly selected for each scenario (T1 and T2) from the total leaves (branch and stool leaves) collected per harvested tree and month and dried at 60 °C. The random leaf sample was ground to fine powder to analyse leaf nutrient concentrations.

C and N were determined through dry combustion analysis using an automated analyser (LECO; mod CN-2000) and P and K by emission spectroscopy using ICP-OES (PerkinElmer, mod. Optima 5300 DV) after acid digestion of the sample in a closed microwave system (Ethos plus). The concentrations of the different elements were calculated on a dry mass basis and expressed as mg g⁻¹ of dry mass.

The Nitrogen Use Efficiency (NUE), defined as the total biomass produced per unit of nutrient absorbed, equivalent to the nutrient concentration in the biomass produced [43] along with the Photosynthetic Nitrogen Use Efficiency (PNUE) were calculated as the ratio of the maximum photosynthetic assimilation to foliar N content.

2.6. Foliar gas exchange measurements

In addition, every month throughout the growing season during the 3 years of the rotation, gas exchange measurements were recorded in both irrigation scenarios (T1 and T2) on two fully expanded mature leaves per tree (three per water scenario) from the top of the canopy between 9 and 11 a.m. A portable photosynthesis system (LCPro+ with Broad Head, ADC BioScientific Ltd., Hoddesdon, UK) was used with a light saturation of 1500 mol m⁻² s⁻¹ obtained using a LED lamp.

We performed stomatal conductance (g_s , mol m⁻² s⁻¹), photosynthetic assimilation rate (A, μmol CO₂ m⁻² s⁻¹) and instantaneous transpiration rate (E, mmol H₂O m⁻² s⁻¹) measurements. Leaf gas exchange measurements were therefore used to calculate the Water Use Efficiency as the ratio between A and E (WUE, in μmol CO₂ mol⁻¹ H₂O) and Intrinsic Water Use Efficiency as the ratio between A and g_s (IWUE, in μmol CO₂ mol⁻¹ H₂O).

2.7. Statistical analysis

The effect of scenarios T1 and T2 on the different variables over the three growing seasons was analyzed using analysis of variance ANOVA (Generalized Linear Model procedure, GLM). Prior to the ANOVA, when normality was not fulfilled, data were transformed using the Box-Cox procedure. Non-parametric local polynomial regression (LOESS) with a smoothing parameter (a) of 0.75 and confidence intervals of 95% was used as a complementary analysis to GLM to analyse differences in the temporal pattern across years as well for variables with non-stable values across the studied period.

All the analyses were performed using the R program [44] and the level of significance was set to p-value < 0.05 for all the analyses. Means were tested using Tukey's test.

3. Results and discussion

3.1. Monthly foliage productivity, distribution and individual leaf area

Many of the traits of the leaves, including the crown architecture, are marked by strong genotypic control [45–48]. However, in the case of the genus *Populus* some morphological plasticities have been demonstrated in response to certain cultural management [47,49]. According to Isebrands and Nelson [50], most agronomic practices, including irrigation, have an impact on the number of leaves, leaf area and leaf display.

Regarding the number of leaves produced during the first year, a clear upward trend over the growing season can be seen in both scenarios, while in years 2 and 3, the number of leaves stabilizes from the second month after leaf emergence (May) as a result of bud flushing on the preformed branches (Fig. 1). The total number of leaves increased 13.6 times from year 1 to the end of the rotation in the optimal scenario. That increase was, however, 10.5 times in the restricted scenario (Fig. 1). The average values for number of leaves over the years of the study are in line with the values obtained by other authors [51] (Table 1). In years 2 and 3 a significant decrease in the number of leaves was observed in the restrictive scenario with respect to the optimal scenario, (p -value = 0.023 and p -value = 0.015 respectively). This reduction was clearly observed in terms of foliar biomass, even in year 1 when there was no reduction in the number of leaves (p -value = 0.667), the W_f reduction between scenarios being 38%, 43% and 30% in years 1, 2 and 3, respectively (Fig. 2). Significant differences were found between both scenarios as regards foliar biomass in years 2 and 3 (p -value = 0.005 and p -value = 0.003), evaluated in the mid-growing season

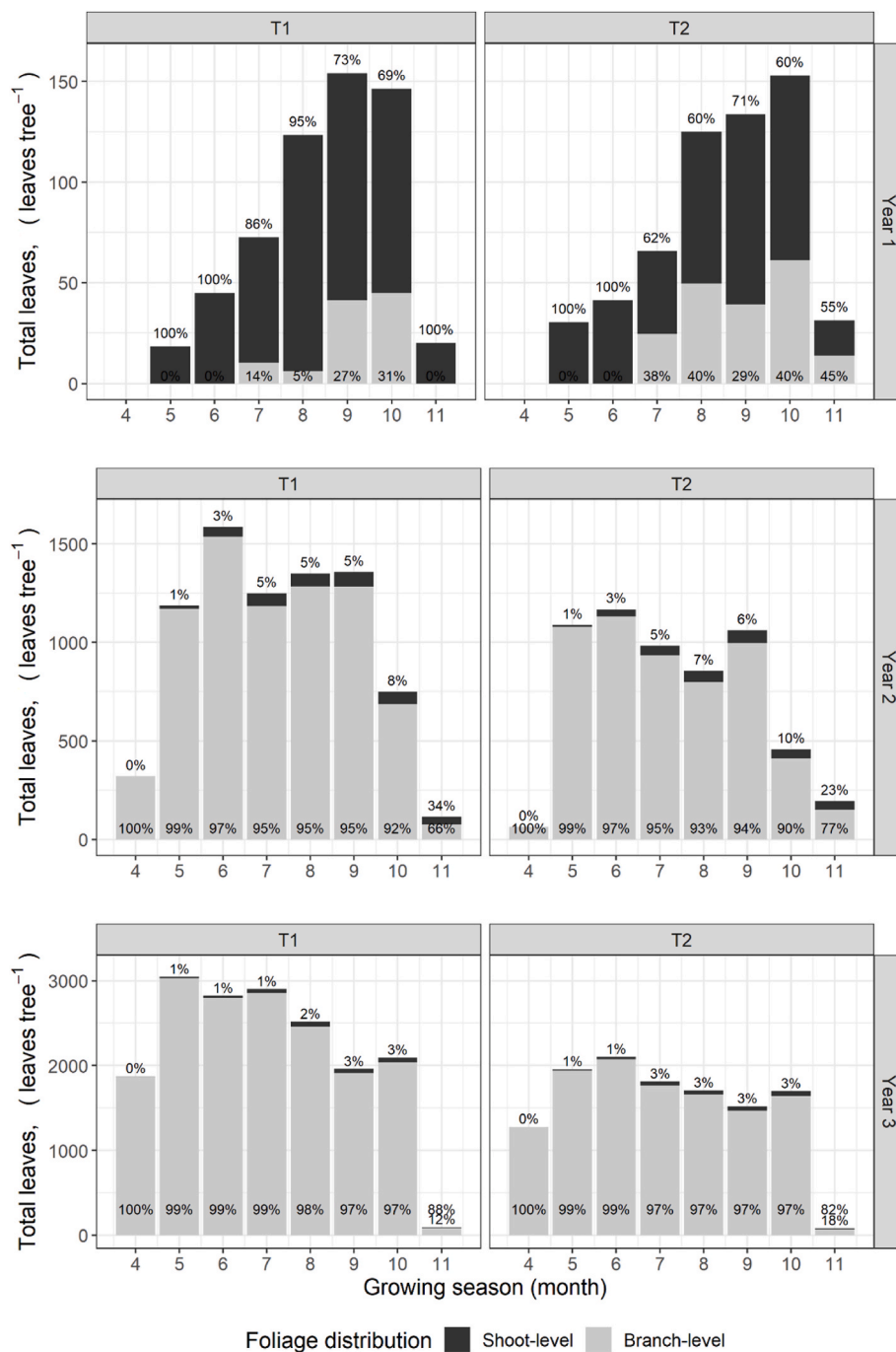


Fig. 1. Monthly leaf distribution and productivity during the first rotation: optimal (Field Capacity (FC)) and restrictive (50% of FC) irrigation scenarios T1 and T2 respectively.

period, LOESS analyses confirming these differences to be significant with a p -value = 0.05.

The spatial distribution of leaves within the tree varies over the growing years. In the establishment year, the leaves grew mostly at stool level in both water scenarios, in contrast to growth in subsequent years once the plantation was established. Furthermore, the leaves were mostly produced at branch level (93% of the leaves come from branches in year 2 and 96.5% in the year 3) (Fig. 1). However, in the first year, the leaf distribution percentages differed between water scenarios. In the optimal scenario (T1) 92% of the leaves were stool leaves, while in the restrictive scenario (T2) that percentage was 82%. Although these differences were not significant (p -value = 0.07), it seems that the category of the leaves differed slightly in this first year. This may have been a

consequence of greater branch production under conditions of water restriction (47% more branches under T2 than T1 in the first year). This increase in branch production, all of which were sileptic in this first year, may have contributed to the success of the establishment in the water restricted plantation. The importance of the sileptic branches in the success of implementation and biomass production has been referred to by Broeckx et al. [51] among others. Smaller leaves as well as a greater number of branches in plantations grown under more severe xericity has previously been reported [52].

In years 2 and 3, the number of leaves at stool level decreased dramatically. The leaves mostly corresponded, in both scenarios, to branch leaves (without differentiating between sileptic and prolectic branches), the proportions being 95% and 98% in T1 for years 2 and 3

Table 1
Foliar biomass (kg tree⁻¹ yr⁻¹) and Number of leaves (leaves tree⁻¹ yr⁻¹) during the first rotation: optimal (T1) and restrictive (T2) water scenarios.

	Scenario	Growing season			Mean values for the whole rotation (mid-growing season)
		1st	2nd	3rd	
W_f (kg tree ⁻¹ yr ⁻¹)	T1	0.11 ± 0.10 c	0.60 ± 0.26 b*	0.83 ± 0.21 a*	0.49 ± 0.4 *
	T2	0.07 ± 0.06 c	0.35 ± 0.14 b**	0.58 ± 0.13 a**	0.31 ± 0.2**
n_l (leaves tree ⁻¹ yr ⁻¹)	T1	98.75 ± 65.68 c	1385.33 ± 404.38 b	2518.50 ± 901.43 a*	1264.5 ± 1085.3
	T2	91.42 ± 59.09 c	1017.00 ± 327.45 b**	1796.78 ± 537.45 a**	893.39 ± 766.1

W_f : Foliar biomass in oven-dry matter; n_l : Number of leaves; T1: Optimal scenario, irrigated to field capacity (FC); T2: Restricted scenario, irrigated to 50% FC.

Different number of * show significant differences between water scenarios for the same year.

Different letters indicate significant differences between years in the rotation for the same water scenario according to Tukey's test (p -value < 0.05).

respectively and 95% and 97% in T2 for the 3rd years. Broeckx et al. [51] reported similarly very small percentages of stool leaves in a 2-year plantation in northern Europe. Under the restrictive water scenario no changes in the spatial distribution of the leaves between stool and branch-level were found beyond the establishment year. Furthermore, it must be borne in mind that individual leaf area is much smaller for branch leaves than for stool leaves [22,51,53]. However, during years 2 and 3, the greater number of leaves at branch-level (more than 95% of the total) means that in general terms, their contribution to the total leaf area of the tree was much greater than that of the stool leaves. Broeckx et al. [51] pointed out that despite stool leaves being less important, both in terms of the number of leaves and the contribution to foliar area, these leaves can be of significant physiological importance due to their high specific leaf area [54], optimal leaf exposition and leaf properties such as lower leaf osmotic potentials to improve water extraction from

drying soil [55,56] and seasonal longevity, since these are the last ones abscised [57].

If we focus on the individual mean leaf area in each of the scenarios over the years, significant differences are observed between years (p -value < 0.0001), the individual leaf area in first year being 56% and 66% higher than the second and third years respectively, probably due to the predominance of leaves at shoot-level (Fig. 3). Although the number of leaves during this first year was basically the same for both scenarios, a reduction in the individual leaf area was observed between the two scenarios, with significant differences being observed in year 2 (p -value = 0.007), although this was not the case for years 1 and 3 (p -value = 0.228 and p -value = 0.123 respectively). The individual leaf area in year 1 was notably lower in the restricted scenario due to the greater presence of branch leaves (104 cm² in the optimal scenario in comparison with 71 cm² in the restrictive scenario, Fig. 3). Numerous studies have documented this reduction in leaf size and weight as a result of water stress [58,59]. In years 2 and 3, the mean individual leaf area is considerably reduced due to the greater presence of branch leaves, which are associated with lower individual leaf area in comparison to leaves located at shoot-level (Fig. 3). This same trend for different *Populus* clones was observed by Al Afas et al. [60], concluding that leaves in the upper canopy layer were larger and heavier, but differed significantly among clones, the mean individual leaf area ranging from 46.37 to 127.67 cm² for the first growing season.

Therefore, although no significant differences in yearly mean leaf area between the two scenarios were detected, these differences were present in the global computation, being visible not only in the change in the spatial distribution pattern of the leaves during the first year, but also the clear reduction in the number of leaves during years 2 and 3, as well as a reduction in their individual leaf area and weight in all the years of the study as a result of water stress. Many authors consider that water availability is one of the core factors affecting poplar foliage production [61–64]. Leaf modifications, such as smaller leaves, were considered adaptive responses under conditions of water stress. Similar observations have been reported by other authors, who point to Mediterranean genotypes of *Populus* developing smaller leaves as an adaptation to drought as well as reduction in leaf biomass production [65, 66].

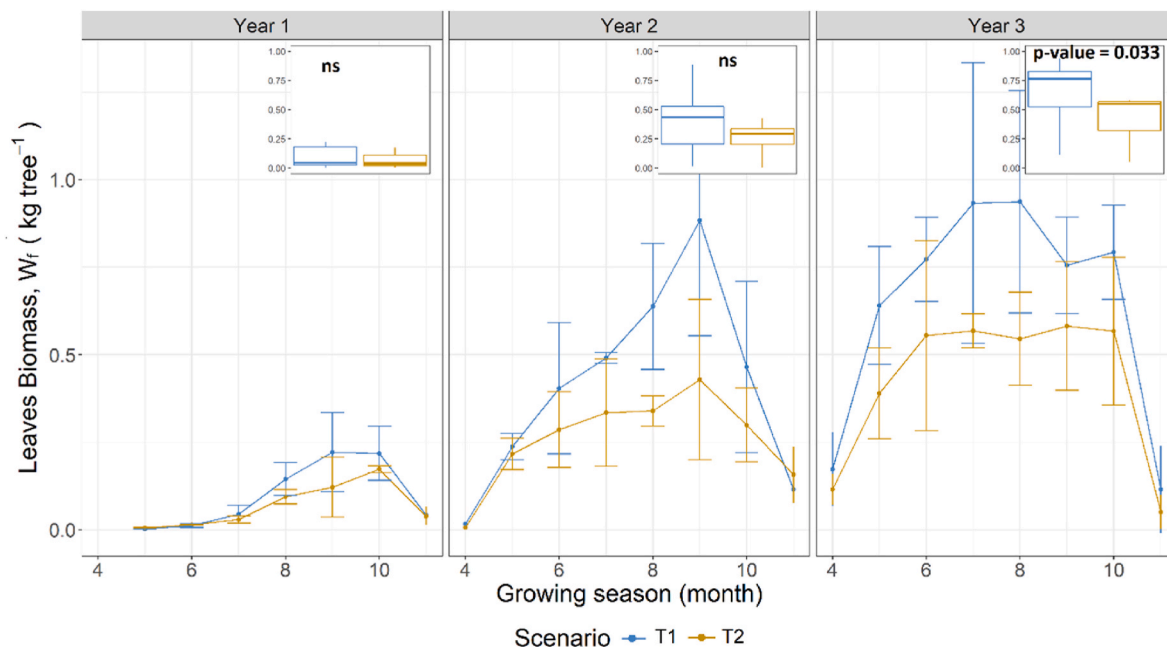


Fig. 2. Monthly dynamics of W_f during the first rotation: optimal (Field Capacity (FC)) and restrictive (50% of FC) irrigation scenarios T1 and T2 respectively. Inset boxplot for the whole growing season, denoting no significant differences as ns.

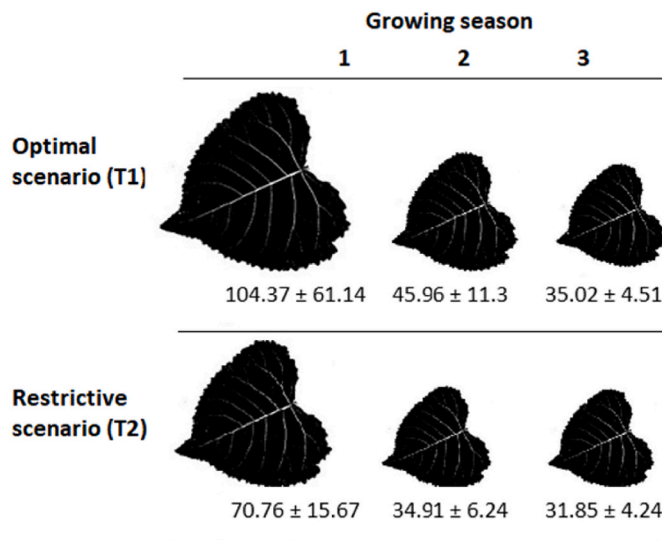


Fig. 3. Evolution of individual leaf area ($\text{cm}^2 \pm \text{sd}$) yearly average during the mid-growing season in the first rotation: optimal (Field Capacity (FC)) and restrictive (50% of FC) irrigation scenarios T1 and T2 respectively. The leaf sizes in the figure are to scale.

3.2. Monthly LAI and SLA analysis

Since differences in the amount and the distribution of the leaf area as well as in the branching patterns have been addressed above, it is also evident that considerable differences in LAI can be found not only over the years, but also between the different water scenarios analyzed in this study.

In the establishment year, the LAI value increased gradually, reaching a maximum (2.39) in late September (Fig. 4). This value is lower than that reported by Tripathi et al. [67] in a Central European plantation (3.6), although it is within the range of the values reported by Al Afas et al. [53], from 2.1 to 5.8, for a variety of genotypes, and is above that reported by Broeckx et al. [68] in a multiclonal plantation in Northern Europe (0.97).

In the restrictive scenario, the LAI pattern was similar to that of the optimal scenario. However, while the same progressive increase was seen over the months, in the restrictive scenario the maximum was reached at the end of October (2.04), one month later than in the case of the optimal scenario, where the maximum value was slightly lower (Fig. 4). However, no significant differences were observed between the different months (p -value = 0.152). The delay in reaching the maximum value under water constraint conditions in this first year is also observed both in the number and weight of leaves (Figs. 1 and 2). This was probably due to the different branch patterns, which as mentioned above was 47% higher in this first year in the case of the restrictive scenario. According to Monclus et al. [28] the LAI_{max} and the magnitude of leaf area reduction were tightly associated with productivity and drought tolerance, these being good indicators of the drought susceptibility of the genotype. This genetic effect along with others associated with the site and management conditions complicate comparison with other studies [28,53,68]. In our study, LAI_{max} values were always lower in the restrictive scenario, although more notable in the 2nd and 3rd growing seasons.

During year 2, the LAI increased rapidly in the first month of the growing season as a result of the flushing of preformed buds. From then on, it continued to increase to its peak at the end of September with values of 7.47. In the last year of the rotation the LAI increased sharply to a peak in the first month of growth, displaying a sustained trend from then until leaf fall. This is probably due to the closure of the canopy, given the high density of plantation. This has also been suggested by other authors, who observed similar trends after canopy closure

explained by increasing self-shading and leaf shedding [68]. In year 2, the LAI_{max} value in T1 was reached in late July at 9.34. There are several studies in which the evolution of the leaf area index over the years has been studied [69–71]. For example, a study conducted in a SRC plantation in Central Europe with similar density reported LAI_{max} values of 3.6, 5.5 and 6.8 during three growing seasons [67], which are lower than those reported in our study for T1. However, another poplar experimental plantation in the USA with a similar density presented higher values during the three years of the rotation of two different poplar clones (2.9, 10, 11 and 1.5, 5.7, 11.6) [72].

In the case of the restrictive scenario (T2), the LAI dynamic was similar, although with significantly lower values (p -value = 0.0002 and p -value = 0.0007 for the years 2 and 3 respectively, these differences being significant as confirmed by the LOESS analyses, with p -value = 0.05). The reduction in irrigation (50% of FC) led to a decrease in LAI_{max} of 50.13% and 34.26%, respectively, for the 2nd and 3rd growing seasons. The LAI_{max} for the restrictive scenario was reached in late September in the 2nd year, as in the optimal scenario. In the 3rd year, the LAI_{max} value was reached earlier than in the optimal scenario, this maximum being in late June (6.14). These findings are in line with those of other studies pointing to the LAI_{max} being severely limited by reduced water availability and development of the canopy, which reduce growth and yield [20,28].

LAI is a key component of biochemical cycles in ecosystems [73] and has an important influence on the exchange of energy, gas and water in trees [74]. The LAI development response under water stress scenarios can be potentially used to better understand the evolution of these plantations under current climate change conditions where water availability may decrease, affecting biomass production. Some authors [48,75,76] have suggested that LAI rather than individual leaf area could be a more reliable indicator of biomass productivity, although both leaf characteristics have frequently been found to be positively correlated with biomass production [28,77–79].

SLA, as well as LAI, is an important structural parameter of forest ecosystems [74] since it is positively related to net assimilation rate [80]. Fig. 4 shows a decreasing SLA trend over the years, the SLA values being slightly lower in the restrictive scenario although no significant differences were observed in any of the years of the rotation (p -value = 0.805, p -value = 0.57 and p -value = 0.271 for years 1, 2 and 3 respectively, these differences being non-significant, as confirmed by the LOESS analyses with p -value = 0.05). Higher initial SLA values (1st month) were observed in both scenarios in comparison to the rest of the months of the growing season (Fig. 4). This could be due to the reported seasonal heterophilia of the genus [81]. Preformed leaves have a different texture and shape to neoformed leaves, the former being harder so as to better withstand spring frosts. The greater SLA detected during the first month of each growing season was probably an indicator that highlights greater foliar surface development in relation to volume [82]. The slight rise in SLA values at the end of the growing season for years 1 and 2 can be explained by the different sample trees considered for the analyses or as a result of a loss of leaf biomass due to nutrient retranslocation (Fig. 4).

The average SLA value during the mid-growing season in the optimal scenario was $12.25 \text{ m}^2 \text{ kg}^{-1}$ in the establishment year, $10.82 \text{ m}^2 \text{ kg}^{-1}$ in the second year and $10.47 \text{ m}^2 \text{ kg}^{-1}$ in the third year. These values were lower than those reported by Al Afas et al. [53] but in line with those reported by Verlinden et al. [76], an overall decrease in SLA with stand aging being identified in both cases.

Although there were no significant differences, the restrictive scenario (T2) showed lower values than the optimal scenario (T1), which is common in plants under water stress [28,35,83,84], with an average value of $11.98 \text{ m}^2 \text{ kg}^{-1}$ in the establishment year, $10.49 \text{ m}^2 \text{ kg}^{-1}$ in the second year and $9.91 \text{ m}^2 \text{ kg}^{-1}$ in the last year of the rotation, presenting the same decreasing trend.

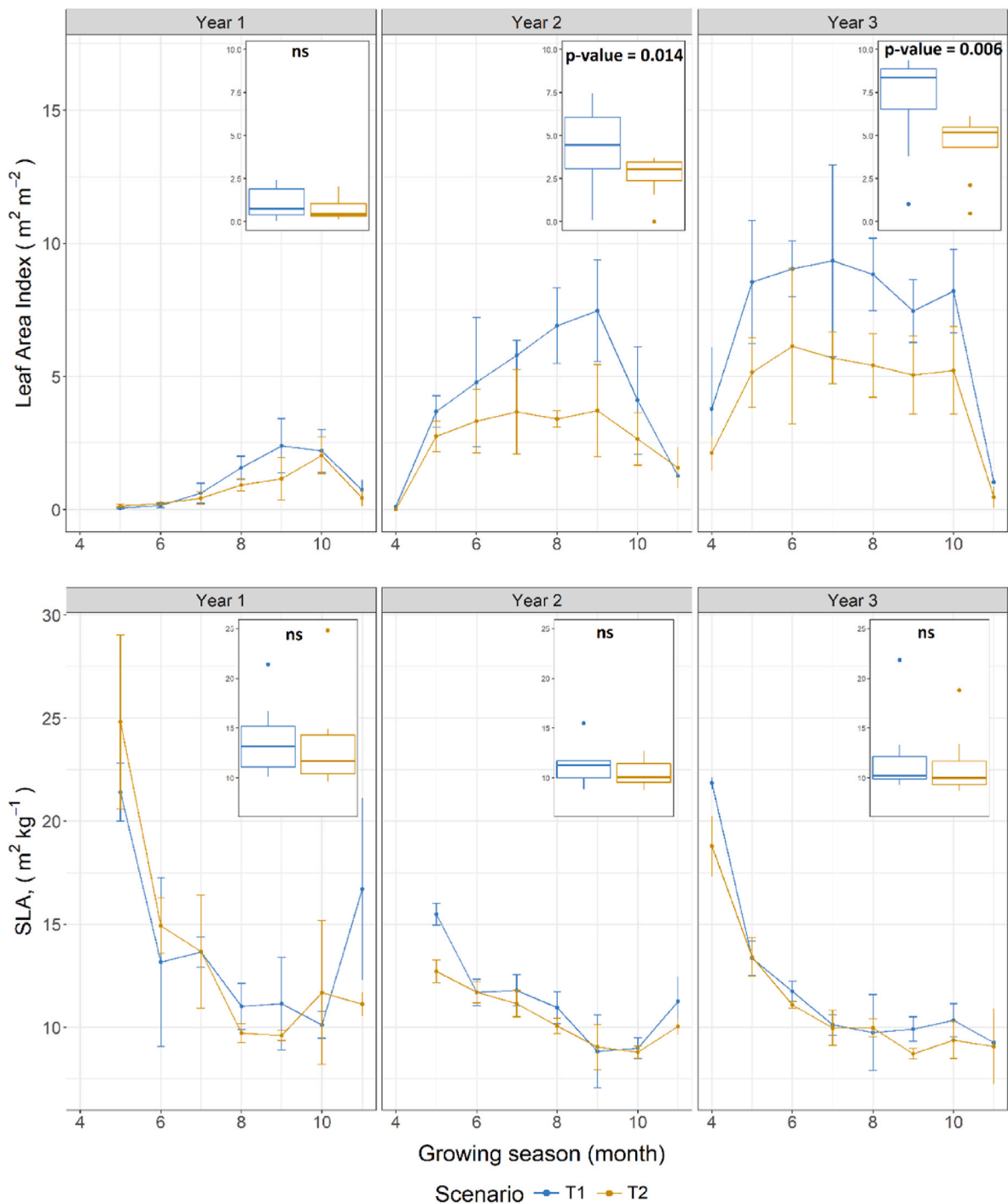


Fig. 4. Monthly dynamics of LAI and SLA during the first rotation: optimal (Field Capacity (FC)) and restrictive (50% of FC) irrigation scenarios T1 and T2 respectively. Inset boxplot for the whole growing season, denoting no significant differences as ns.

3.3. Monthly dynamics of foliar nutrient concentrations: carbon, nitrogen, phosphorus and potassium

A decrease in nutrient concentration was observed between the initial and senescent leaves (Fig. 5) of around 56% for N, 75% for P and 54% for K, with an average percentage for the three years. Therefore, foliar nutrient concentrations change dynamically with canopy growth, an expected, strong seasonal variation with decreasing trends being observed over the different growing seasons. The magnitude of these variations leads us to rethink leaf nutrient characterisation protocols and the effect of leaf age on the variability observed in some species

[85].

The lower foliar concentrations of N and P at the end of each growing season would indicate high efficiency in the reabsorption of those nutrients prior to leaf abscission. Nutrient mobility, however, may sometimes be masked by dilution effects due to increased carbohydrates in the leaf, resulting from very strong photosynthetic activity [86].

However, this trend was not observed in K, perhaps due to lower requirements for this nutrient or less limitation in the ground, which would imply less need for retranslocation.

The gradual decrease in NPK observed over the whole growing season has often been described as the translocation of these highly mobile

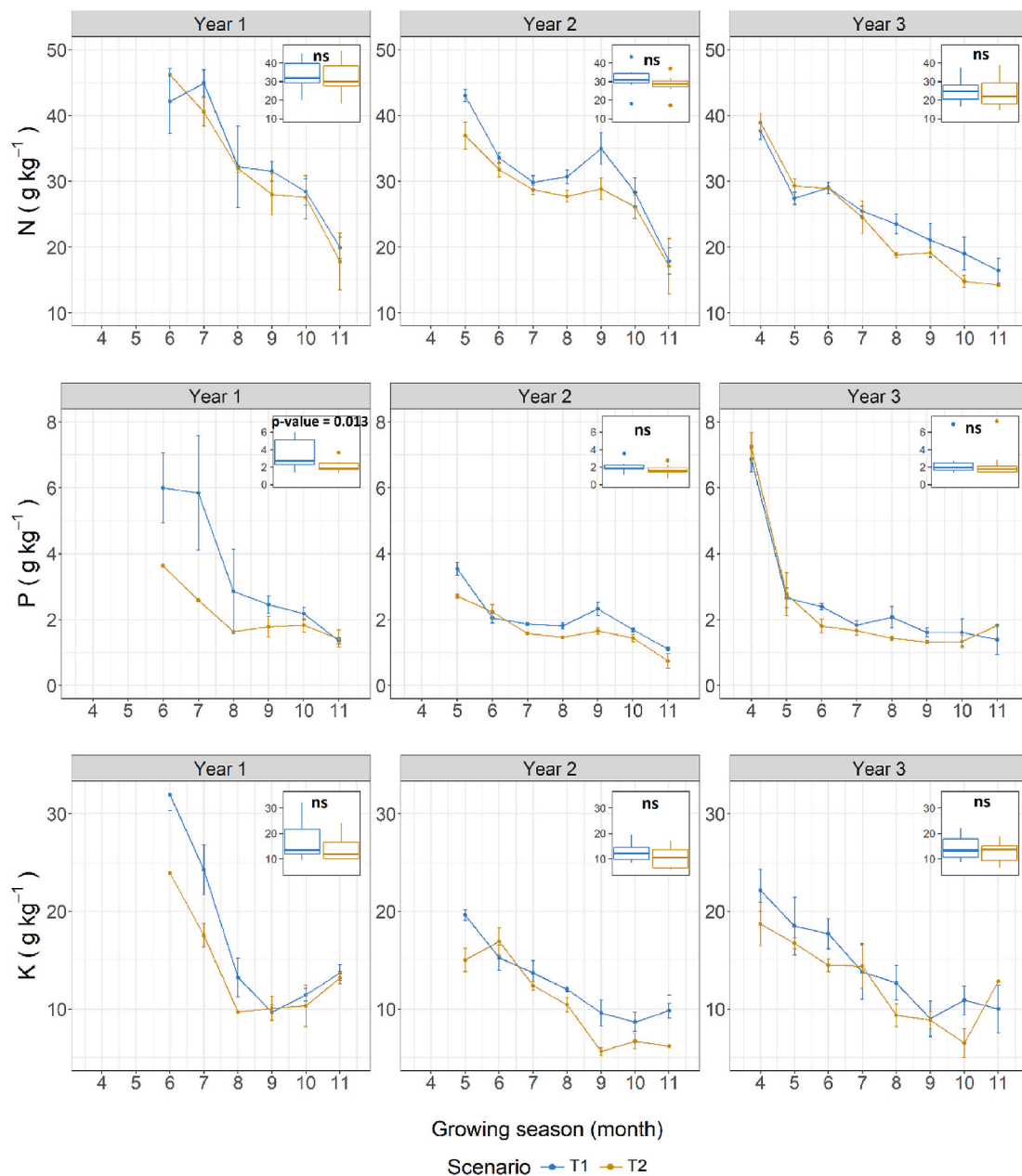


Fig. 5. Monthly dynamics of N, P and K leaf concentration during the first rotation: optimal (Field Capacity (FC)) and restrictive (50% of FC) irrigation scenarios T1 and T2 respectively. Inset boxplot for the whole growing season, denoting no significant differences as ns.

nutrients from the more mature leaves to the woody above and below-ground biomass of the tree [87].

However, as in the case of this study, reabsorption can also occur from the first leaves during the growing season [88]. This translocation is especially intense in highly productive deciduous species such as poplar [89]. The greater translocation observed for P could also suggest a greater limitation of this element as observed by Ozbucak et al. [90] in *Corylus avellana*. L plantations. Our study area presents very poor initial values of assimilable P in the soil (9.35 mg kg^{-1}). Wu et al. [91] identified an adequate P level as being between 10 and 40 mg kg^{-1} . The basic pH of the study area leading to the formation of calcium phosphate precipitates results in low P solubility, which may add to the increased translocation [92].

Harvey and Van de Driessched [93] also observed an important decrease in hybrid poplar NPK concentrations between mature leaves (August) and senescent leaves (November) of around of 60% for N, 12% in the case of P and 16% for K. In riparian ecosystems, González et al.

[94] also found gradual decreases in foliar concentrations of N and P in the *Populus* genus throughout the entire growing season.

Under the restrictive scenario (T2), a similar dynamic was observed, with a decrease of 59.5% for N, 69.5% for P and 45.1% for K. The retranlocation observed in P and K was therefore slightly lower. This could be due to the greater susceptibility of the species to drought conditions, which affects the restranlocation of nutrients [95,96]. This behavior has been considered a mechanism to increase osmotic regulation [93], especially in the case of P and K given the important role of these nutrients in osmotic regulation, stomatal control and water use efficiency [97].

The foliar C concentrations, both in the optimal and restricted scenarios, showed a less marked decrease between the initial and final growing season, due to the low mobility of this element. The average percentage decline over the three years was slightly higher in the restricted water scenario (7.9%) compared to the optimal water scenario (6.0%).

In mature leaves (mid-growing season), a gradual and significant inter-annual decrease in the concentrations of N and P were observed for both water scenarios mostly as a result of the higher demand derived from tree growth. In the case of K concentration, however, a gradual decrease was not observed over the rotation period, a slight increase in K concentration being observed in the third year compared to the second year of the rotation (Table 2).

The high mean concentrations of nutrients during the mid-growing season, especially K, detected in the initial year of our study in mature leaves compared to the following two years of rotation, are due to the high concentrations obtained in June and July of the establishment year (Table 2). In that period, absorption from the soil and the retranslocation of nutrients from the root and stem to developing leaves occur, this retranslocation being especially notable in the case of K, since it is a very mobile element [97].

The foliar concentrations of C in mature leaves hardly varied over the whole rotation cycle for both water scenarios (Table 2). Similar results were obtained by Tripathi et al. [34] and Kanwal et al. [98] under controlled greenhouse conditions. The accumulation of C in the leaf was a consequence of the photosynthetic balance and leaf respiration. Drought conditions lead to a decrease in gas exchange, which causes a decrease in the net gain of C and a reduction in growth, associated in turn with a lower C investment [99], so that C will remain in equilibrium regardless of water availability [100].

In the restrictive scenario (T2), throughout the years of the rotation, the mean concentrations of NPK in mature leaves (mid-growing season) were lower than those obtained in T1, these differences only being significant in the case of P, and of N in the intermediate year (Table 2). This decrease was more pronounced for P (28.3%) and K (17.7%) than for N (8.3%), probably due to the lower mobility of P and K under restricted water conditions [101] and the lower root absorption due to reduced soil water availability, as suggested by Diaz and Roldan [102] and Meng et al. [103]. This would also imply a reduction in soluble forms of P and K in the soil [104]. Similar results between different water scenarios in poplar SRC plantations have been obtained by Tripathi et al. [34], who reported decreases in NPK foliar concentrations under drought conditions of around 8%, 21% and 17%, respectively.

Nitrogen Use Efficiency (NUE) showed a progressive and significant increase throughout the whole rotation in both water scenarios

Table 2

Mean values ± sd of C, N, P and K concentration in mature leaves (mid-growing season) during the first rotation (3 years) in optimal (Field Capacity T1) and restrictive (T2) water scenarios.

	Scenario	Growing season			Mean values for the whole rotation
		1st	2nd	3rd	
C (%)	T1	44.08 ± 1.19	44.29 ± 1.12	44.07 ± 0.96	44.15 ± 1.06
	T2	44.66 ± 8.25	44.29 ± 1.32	44.32 ± 12.71	44.41 ± 1.21
N (g kg ⁻¹)	T1	37.69 ± 7.11a	32.27 ± 2.50a*	24.77 ± 3.32b	31.57 ± 7.09
	T2	34.77 ± 6.83a	29.26 ± 1.84a**	22.87 ± 4.50b	28.63 ± 6.65
P (g kg ⁻¹)	T1	4.29 ± 2.00 a*	2.01 ± 0.24 b*	1.97 ± 0.35 b*	2.76 ± 1.59*
	T2	2.16 ± 0.68**	1.73 ± 0.33**	1.55 ± 0.23**	1.79 ± 0.49**
K (g kg ⁻¹)	T1	19.77 ± 9.38	12.63 ± 2.39	13.29 ± 3.68	15.23 ± 6.66*
	T2	13.58 ± 5.20	11.34 ± 4.29	11.77 ± 3.03	12.15 ± 4.18**

Different number of * show significant differences between water scenarios for the same year.

Different letters indicate significant differences between years in the rotation for the same water scenario according to Tukey's test (p-value < 0.05).

Table 3

Mean value ± sd of NUE and PNUE in the mid growing season during the first rotation (3 years) in optimal (Field Capacity T1) and restrictive (T2) water scenarios.

	Scenario	Growing season			Mean values for the whole rotation
		1st	2nd	3rd	
NUE (g g ⁻¹)	T1	73.90 ± 29.42c	139.60 ± 17.00b*	314.61 ± 75.10a*	167.89 ± 109.32
	T2	75.16 ± 27.20c	117.55 ± 19.86b**	240.08 ± 46.19a**	139.45 ± 74.45
PNUE (µmol g ⁻¹ s ⁻¹)	T1	3.76 ± 1.53c	5.60 ± 1.24b	7.06 ± 1.77a	5.38 ± 1.99
	T2	3.16 ± 2.23	5.24 ± 1.25	5.65 ± 2.68	4.69 ± 2.27

Different number of * indicate significant differences between scenario in the same year and different letters indicate significant differences between years in the same scenario according to Tukey's test (p-value < 0.05).

(Table 3). NUE tended to increase as nitrogen availability decreased [105,106], as observed in this study, where soil N contents were low, and fertilization was not applied during the rotation.

NUE, however, decreased under water restriction, this decrease being especially notable in years 2 and 3 when the effect of stress was more evident. This decrease is in line with that previously reported by Liang et al. [107]. In all cases, the nitrogen use efficiency values were highly dependent on the site conditions and the genotype [108,109].

The Photosynthetic Nitrogen Use Efficiency (PNUE) increases significantly in the optimal irrigation scenario throughout the rotation (Table 3), which would indicate a greater amount of N invested in the photosynthetic activity for the production of greater biomass [110]. In the restricted irrigation scenario, however, the increase was not significant, with the PNUE values being lower in the initial year compared to the 2nd and 3rd, in which similar mean values were found. This may indicate an optimization of foliar N invested in photosynthesis in the last year of the rotation when the water stress is more pronounced.

No significant differences in PNUE were found between the two water scenarios, although in the 3rd year of rotation the mean values were notably lower in the restrictive irrigation scenario compared to the optimal scenario. Under drought conditions, NUE and WUE were closely linked to stomatal closure, which will lead to an increase in IWUE and a decrease in PNUE [111,112]. In the restrictive irrigation scenario, IWUE was significantly higher than in the optimal scenario (Table 4), which should therefore mean lower PNUE values. However, this only occurred in the last year of the rotation, indicating that in the first two years of water restriction, higher IWUE would not entail a cost at photosynthetic level as a consequence of a greater mobilization of N to the photosynthetic apparatus, this being characteristic of deciduous species with short leaf life [113]. According to our results, high PNUE values could

Table 4

Mean value and standard deviation of intrinsic Water Use Efficiency (IWUE) and Water Use Efficiency (WUE) during the first rotation (3 years) in optimal (Field Capacity T1) and restrictive (T2) water scenarios.

	Scenario	Mid-growing season		
		1st	2nd	3rd
IWUE	T1	29.71 ± 9.87b*	54.59 ± 24.1a*	55.72 ± 20.05a*
	T2	69.73 ± 30.96**	78.88 ± 25.65**	71.71 ± 24.44**
WUE (µmol CO ₂ mol ⁻¹ H ₂ O)	T1	2.08 ± 0.74 b	5.96 ± 1.03 a	5.47 ± 0.94 a
	T2	2.31 ± 0.86 b	5.38 ± 1.13 a	5.77 ± 0.61 a

Different number of * show significant differences between water scenarios for the same year.

Different letters indicate significant differences between years of the rotation for the same water scenario according to Tukey's test (p-value < 0.05).

therefore be associated with a greater tolerance to situations of water deficit, indicating that N use efficiency could mean an important functional advantage under restrictive conditions, as previously reported by Ref. [114].

3.4. Monthly dynamic responses of leaf gas exchanges

The photosynthetic rate (A) recorded throughout the growing season under optimal irrigation was highly variable (Fig. 6). This might be expected when dealing with instantaneous measurements over a long period of time with environmental fluctuations in temperature, irradiance or humidity [115]. In any case, instantaneous measurements of photosynthesis should be seen as general trends, otherwise they can be misleading [116]. Values higher than $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ were recorded in most months with peaks of $22 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is comparable to rates previously reported for this genotype in similar environments [83]. Among woody plants, poplar trees are known to show high photosynthetic capacity although they also exhibit high genotypic variation within the genus [117]. The A values range, for example, from 5 to $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ reported by Luukkanen and Kozłowski [118] in *Populus nigra* L. to $20\text{--}22 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *Populus trichocarpa* Torr. & A. Gray ex. Hook. cited by Wiard [119].

In the mid-growing season, when the maximum vegetative activity occurs, higher mean A values under optimal water conditions were detected in years 2 and 3 of the rotation ($16.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) in comparison to those observed in year 1 ($11.1 \mu\text{mol m}^{-2} \text{s}^{-1}$). This is probably due to the temperature and humidity conditions recorded in year 1, which led to a greater deficit in CO_2 concentration (ci). The g_s values in this scenario dropped sharply in relation to the remaining months of the following years of the rotation (to around $0.36 \text{mol m}^{-2} \text{s}^{-1}$), coinciding with the higher temperatures that characterize this climate during these months (35°C maximum mean temperature and 76651Kj m^{-2} global radiation at the plantation site). In fact, this stomatal conductance was similar to that observed under Mediterranean conditions in the absence of irrigation [120].

The monthly oscillations of A and g_s in the two water scenarios (T1 and T2) often ran in parallel, although the values were always lower in the restricted water scenario. Thus, mean g_s values were significantly lower in T2 during the three growing seasons (Fig. 6) and especially in the mid-growing season, indicating that stomatal closure occurred. The A values also declined, although less notably. The greater decrease in g_s compared to that of A in the restricted water scenario points to the possibility of applying less water through strategies aimed at increasing efficiency. This possibility has previously been explored in poplar plantations including this genotype by Gonzalez-Gonzalez et al. [83].

In the months of maximum growth, intrinsic water use efficiency (IWUE) as well as transpiration efficiency (WUE) were significantly higher in years 2 and 3 of the rotation compared to the establishment year under both water scenarios (Table 4). These differences are attributable to significantly lower A in the initial year (p -value = 0.001 and < 0.00001 in T1 and T2 respectively, these differences being significant as confirmed by the LOESS analyses at $p = 0.05$) rather than to differences in stomatal conductance (p -value 0.5729 and 0.1566), which was similar in the three periods of each water scenario. Photosynthesis is a combination of diffusive and biochemical process and is limited by both stomatal as well as non-stomatal factors such as mesophyll conductance, carboxylation and photochemistry [121]. Furthermore, the density-driven change in photosynthetic photon flux and the changes in stomatal conductance can occur at different time scales, the former being much faster [122].

Under restrictive water conditions, IWUE was always significantly higher than under optimal irrigation in any of the years of the rotation (p -value < 0.0001), denoting greater instantaneous gain of carbon in relation to water loss. The observed decreases in conductance were always far greater (about double the percentage) than those observed in the rate of A. In any case, the mean photosynthesis values under this

restrictive scenario remained high in the maximum period of tree activity ($11.1 \mu\text{mol m}^{-2} \text{s}^{-1}$). The values obtained in relation to IWUE were indicative of the capacity of the leaf to regulate photosynthesis and stomatal conductance and therefore the suitability of the genotype for adaptation to restrictive water conditions endured over time. This strategy to increase efficiency therefore avoids dehydration and could constitute long-term acclimatization, contributing to prioritizing carbon gain.

Even though the transpiration rate was significantly lower in the restrictive scenario (Fig. 6), WUE values did not, however, show significant differences between water scenarios, revealing that for a given stomatal opening, the transpiration rate can be highly variable, depending on the set of environmental factors such as humidity, temperature, radiation and wind speed [123].

Based on these findings, the genotype 'AF2', identified as highly productive in different scenarios [40,83,124], showed tight stomatal control over water restriction, maintaining high photosynthetic levels, which is associated with some degree of isohydricity. The isohydric or anisohydric behavior of different poplar genotypes and therefore of different strategies to tackle water scarcity has previously been reported [125,126]. Regulation of water status may be critical in terms of survival or mortality under drought events [127]. In this regard, the survival rates under the restrictive water scenario were very high (100%) with no symptoms of defoliation, which highlights the ability of 'AF2' to survive in these environments, as previously reported in other studies conducted under Mediterranean conditions [83].

4. Conclusions

Detailed monthly foliar analyses under different water scenarios could help to better understand poplar plantations, contributing to improve biomass models, future breeding programs and promote these plantations under Mediterranean conditions where irrigation could be restricted in the context of climate change.

The findings of this study point to different behavioural patterns of variables in foliar dynamics of a poplar short rotation plantation under different water scenarios (an optimal scenario with irrigation to field capacity and a restrictive scenario with irrigation to 50% of the field capacity), as along with differing dynamics of the plantation over the three years of the rotation cycle.

The spatial distribution of leaves varies over the growth years studied, with most leaves appearing at stool level in the first year whereas in years 2 and 3 leaf production occurs at branch level. This behavior is explicitly reflected in the individual mean leaf area for the three years of the rotation cycle, this variable being clearly greater in the first year (104cm^2) and then stabilizing in subsequent years at 35cm^2 .

Under conditions of water restriction, clone 'AF2' adopted a strategy of producing 47% more branches in the establishment year, displaying a different behavior in the distribution of leaves with a lower percentage of stool leaves. Water restriction led to a decrease in leaf biomass, even in year 1, where leaf production (number of leaves) was exactly the same in both scenarios.

The LAI dynamic observed is similar for the three years of the rotation cycle, the LAI_{max} being 2.39, 7.47 and 9.34, respectively. The LAI response under water stress scenarios can potentially be used to better understand these plantations, the results of our study pointing to significantly lower values after the establishment year in the restrictive scenario, that is, a decrease in LAI_{max} of 50.13% and 34.26% in the restrictive scenario for the 2nd and 3rd growing seasons.

A downward trend in the SLA is observed throughout the years of the rotation, although no significant differences are detected between water scenarios despite the fact that the average is lower in the restrictive scenario. A decrease is observed for NPK foliar concentrations and PNUE values over the three years of the rotation, lower values being observed under water restriction. In contrast, IWUE values are significantly greater under water restriction, these being indicative of the suitability

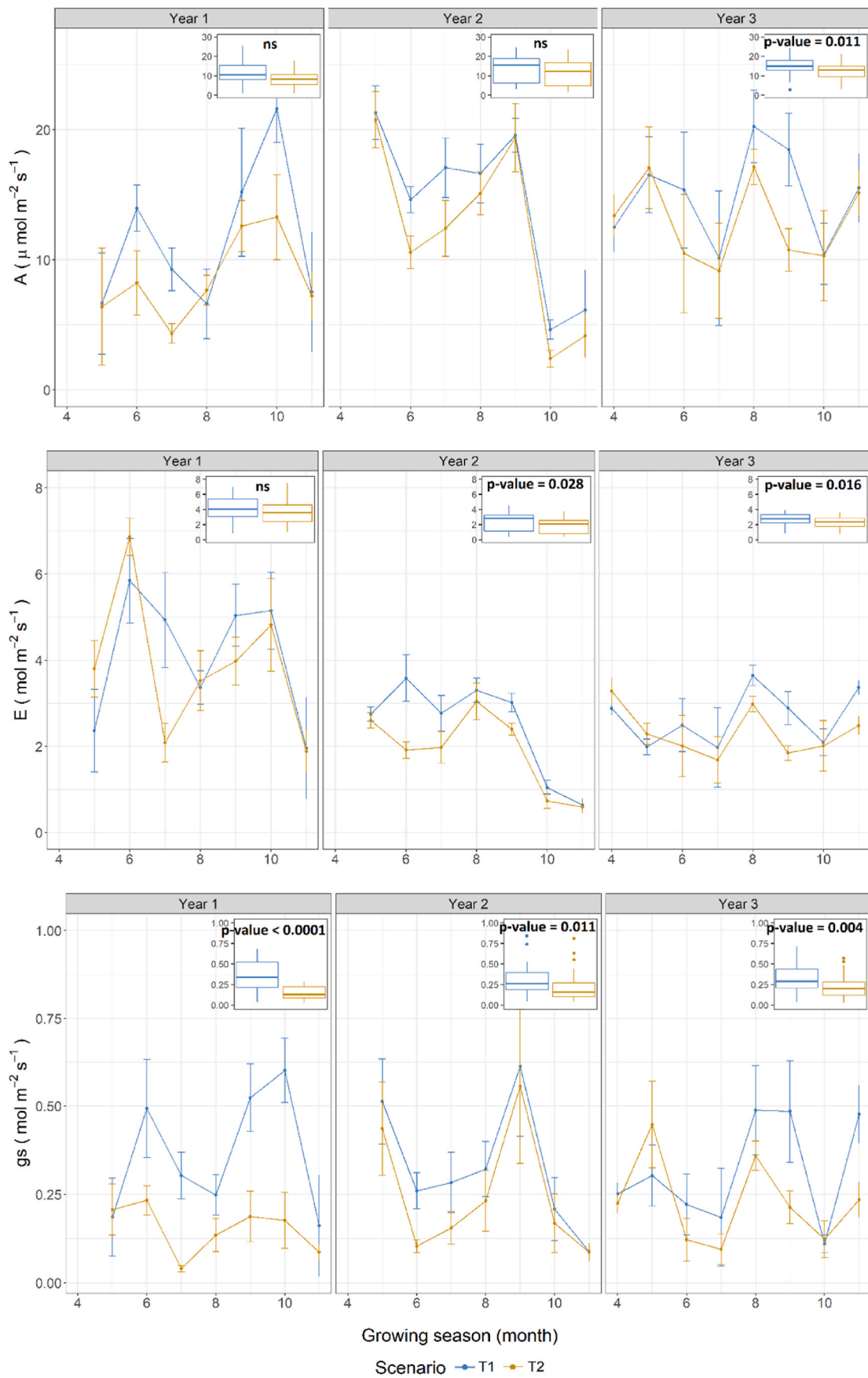


Fig. 6. Monthly dynamics of A, E, g_s during the first rotation: optimal (Field Capacity (FC)) and restrictive (50% of FC) irrigation scenarios T1 and T2 respectively. Inset boxplot for the whole growing season, denoting no significant differences as ns.

of the genotype for adaptation to longer term restrictive water conditions.

Gas exchange results, considered representative of what may occur at plant level, suggest that the selected genotype 'AF2' has tight stomatal control under conditions of water stress, maintaining high photosynthetic levels, which is associated with some degree of isohydricity. This genotype adopts strategies which mitigate losses in production under climate change scenarios. Hence, besides being of interest for breeding programs, this behavior makes it a good candidate for use in modeling behavior for biomass production in poplar short rotation plantations given its positive response under different water restriction scenarios.

The information provided corresponds to a specific clone 'AF2'. Further studies including other genotypes would be of interest to compare different clone responses.

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