

## PHYSIOLOGICAL ADAPTATION OF EUROPEAN BEECH (*FAGUS SYLVATICA* L.) AND WILD CHERRY (*PRUNUS AVIUM* L.) SAPPLINGS AFTER WINDTHROW

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### Abstract

Variations in some physiological parameters of European beech (FS) and wild cherry (PA) saplings were studied in the second (2016), fifth (2019), and seventh year (2021) after windthrow disturbance in a monodominant European beech forest. Net photosynthetic rate ( $A_N$ ), transpiration rate ( $E$ ), water-use efficiency ( $WUE$ ), and total chlorophyll content ( $TCC$ ) of FS and PA saplings were measured both in a windthrow site (W) and in a closed-canopy site (C). The physiological measurements in C-site were used as a control for the comparisons with W-site. European beech leaves on W-site had a positive photosynthetic response to higher light intensity only in 2019, while in the wild cherry leaves, similar increase was observed in 2016 and 2021. At the end of the study period,  $E$  of FS and PA leaves were equalized between W-site and C-site and between the two species. However, two years after windthrow, FS saplings had a similar transpiration rate in the two sample sites, while PA saplings had significantly higher transpiration in the W-site. In 2019, FS leaves managed to increase its  $E$  in windthrow site, but it remained high in the PA's leaves.  $WUE$  remained unchanged in W-site at the beginning of the experimental period for both species, but this physiological parameter was significantly higher in FS saplings. In 2019, the  $WUE$  in FS leaves was stabilized, while in the PA leaves, it even increased. In 2021, both species had stable levels of  $WUE$ . In W-site, the FS leaves had the same  $TCC$  throughout the experimental period, while such a parameter was higher in W-site in the PA leaves. Better physiological adaptation of PA to changed microclimatic conditions after the windthrow disturbance is probably the main reason for this species' pioneer character and rapid colonization of the territory. The protective role of herbaceous plants, which invade in a windthrow site, allows FS to save the physiological activity and even increase physiological processes and parameters a few years after disturbances.

**Key words:** photosynthesis, total chlorophyll content, transpiration, water-use efficiency.

### Introduction

Windthrow in a forest is a natural process, which is repeated element in the forest dynamics. While canopy gaps may alter

many features of understory microenvironments, their most obvious effects are on understory light regimes. However, even in large gaps, the potential duration of high light levels from direct radiation is

relatively brief and limited to a much narrower range of incidence angles than at an open site (Canham et al. 1990), especially on a northern slope. The relatively brief duration of high light levels provides only a limited time of high potential carbon gain to recover the synthesis and maintenance costs of physiological and morphological acclimation to high light (Canham et al. 1985). Thus, windthrow gaps pose a serious limitation on the sapling's adaptation to high incident light levels.

It has been frequently noted that pioneer and early successional species have higher potential growth rates than tree species capable of responding to small disturbances (Bazzaz 1973, Berry 1975, Chabot 1977, Patterson et al. 1978, Ulanova 2000, Rich et al. 2007). According to Bazzaz (1979), early successional species will have higher physiological flexibility relative to that of species found in later successional habitats. Shade-intolerant species are thought to allocate more resources to rapid growth, especially height growth, instead of overall structural strength. Some authors reported rapid increase in the growth rate of early successional trees when the canopy above them is removed (Marks 1974). Shade-intolerant, fast-growing, short-lived pioneer species (such as wild cherry) should have lower biomechanical safety margins than shade-tolerant, long-lived species of comparable stature (Givnish 1995).

The late-successional species, such as European beech, are considered shade-tolerant (San-Miguel-Ayanz et al. 2016, Leuschner and Ellenberg 2017), and their regeneration under intense light is difficult (Collet et al. 2001, Ramírez-Marcial et al. 2010, Malík et al. 2014). Emborg (1998) established that relative light intensity (RLI) increased to about 10 % in beech forest's gaps and

made regeneration of European beech possible, but its saplings did not survive at RLI below 2 %. As Szwagrzyk et al. (2001) points out, even in a strongly shade-tolerant species, like beech, the formation of a seedling bank required the occurrence of canopy openings nearby. According to Ammer (1996), on the shelterwood and the clear-cut plots within the beech forest, height and height increment of European beech and sycamore maple saplings increasingly depend on intra- and interspecific competition effects. In the clear-cut plot, the natural regeneration had consisted almost exclusively of even-aged sycamore maple saplings, which were already established before the cutting and had access to full light (Ammer 1996). Mountford et al. (2006) found that the seedling density in beech forests is highest at the gap edge or just outside the gap. In contrast, the highest plants were recorded in the gap center by Ritter et al. (2005), corresponding to the increased resource availability there.

Many factors may limit tree saplings height within the windthrow patches. Higher illumination leads to increased air temperature and decreases air, and soil water availability provokes reduced water regime and decrease in photosynthetic activity due to leaf damage (Reynolds and Frochot 2003). Stomatal conductance is also negatively affected by light increasing (Tognetti et al. 1997), in addition to drought effects, which leads to a decrease in water-use efficiency.

The present study's main objective was to examine whether an early successional species such as the wild cherry adapts its physiological processes faster and more successfully than a late succession species such as the European beech to a changed microenvironment after windthrow.

## Materials and Methods

### Site description and plant material

The effect of natural disturbance (windthrow) on gas-exchange, water relation, and chlorophyll content of European beech (*Fagus sylvatica* L.) and wild cherry (*Prunus avium* L.) saplings were studied in Western Balkan Mountains. The measurements were conducted in July 2016, July 2019, and July 2021 at the Petrohan Training and Experimental Forest Range. Eighteen months before the first measurements (December 2014), a stand dominated by the European beech was affected by the windthrow. On a total area of 6 ha, almost all 80-years-old beech trees were uprooted or broken seriously by the snow and wind.

In the summer of 2016, a sample site of 0.1 ha (25×40 m) was set up in part of the stand affected by the windthrow (W-site) and another 0.1 ha (25×40 m) sample site – in the adjacent undisturbed, closed-canopy area (C-site), which was used as a control (Table 1).

**Table 1. Sites description of windthrow site (W-site) and closed-canopy site (C-site).**

Sites description	W-site	C-site
Latitude	43°11'19" N	43°11'4" N
Longitude	23°7'30" E	23°7'47" E
Altitude, m	862	870
Slope, °	24	20
Aspect, °	54 (NE)	62 (NE)

Note: Latitude, longitude, and altitude were measured with a GPS-device (Garmin Ltd., Schaffhausen, Switzerland). Slope and aspect were measured in a software MapSource v. 6.16.3 (Garmin Ltd., Schaffhausen, Switzerland).

Microclimatic conditions of sample sites were determined during the physiological measurements. Photosynthetic Photon Flux Density (PPFD,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) was

measured with a Li-190 Quantum sensor (Li-COR, Bioscience, Ltd., Lincoln, USA);  $\text{CO}_2$ -concentration (ppm), air temperature ( $T_{\text{air}}$ , °C) and relative air humidity (RH, %) were measured with internal sensors of the Portable photosynthesis system Li-6400 (Li-COR, Bioscience, Ltd., Lincoln, USA).

### Physiological measurements

The measurements were conducted in the second (2016), fifth (2019), and seventh (2021) year after windthrow disturbance, in typical clear-sky July days, between 9:30 and 11:30 AM. Net-photosynthetic rate ( $A_N$ ) and transpiration rate ( $E$ ) were measured using an LI-6400 portable photosynthesis system (Li-COR, Bioscience, Ltd., Lincoln, USA) on two mature leaves, selected between 3rd and 5th leaf from the top of fifteen saplings in each site (Tausz et al. 2003). Before measurements, the instrument was calibrated according to standard procedures (LiCor 2012). Measurements were taken under controlled conditions within the chamber: saturated PAR of  $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ; ambient for experimental variants leaf temperature and  $\text{CO}_2$  concentration; relative air humidity at 40 to 45 % resulting in a leaf-to-air vapor pressure deficit ranging from 1.17 to 1.37 kPa; flow rate of  $500 \mu\text{mol}\cdot\text{s}^{-1}$ . Water-use efficiency ( $WUE$ ) was calculated using the formula:  $WUE = A_N \cdot E^{-1}$  (Larcher 2003). Total chlorophyll content ( $TCC$ ) was determined with portable chlorophyll meter AtLEAF+ (FT Green, LLC, Wilmington, USA).

### Statistical analysis

Shapiro-Wilk test was used to determine whether the outcome variables were normally distributed. A two-tailed T-test was

used to determine the significant difference between the environmental conditions in W-site and C-site. The two-way ANOVA (Factor A: Species and Factor B: Conditions) was used to test the significant difference among the variants within each year. A multiple-comparison procedure (Tukey Test) was used to test the statistical significance of differences among the variants. All statistical procedures were performed with MS Excel and user-defined functions in Visual Basic for Applications (MS VBA 7.1, Microsoft, Redmond, WA, USA). Only statistically significant results (as defined by a  $p$ -value < 0.05) were discussed.

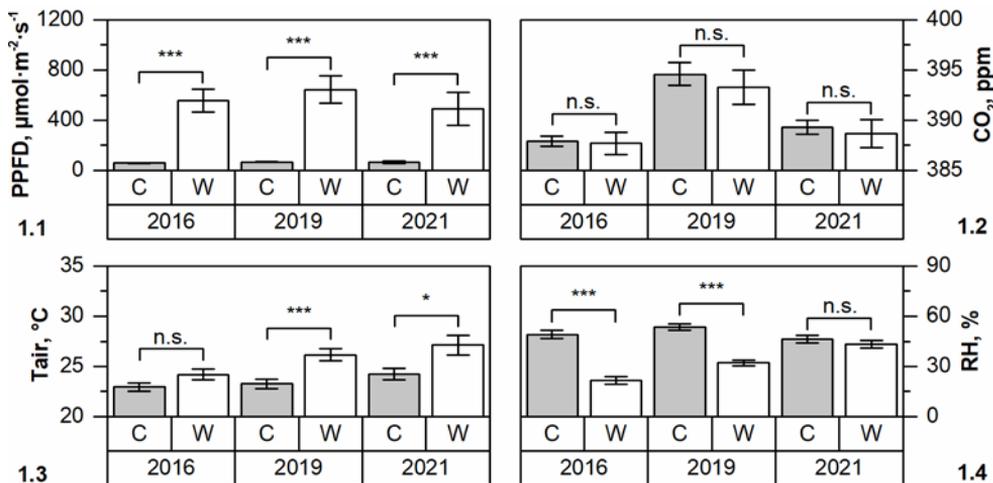
## Results and Discussion

### Micro-climatic conditions

The environment factor most strongly affected by the windthrow was the illumina-

tion. In 2016, it was 9.47 times higher in the W-site as compared to the C-site ( $T = 5.53$ ,  $p$ -value < 0.001), 9.73 times in 2019 ( $T = 5.24$ ,  $p$ -value < 0.001), and the difference decreased to 7.69 times in 2021 ( $T = 3.20$ ,  $p$ -value = 0.003), mainly due to the growth of the crowns of some remaining adult beech trees, as well as some PA individuals (Fig. 1).

The variation in the relative humidity between sites was lower in the W-site compared to the C-site 2.27 times in 2016 ( $T = 8.49$ ,  $p$ -value < 0.001), the difference decreased to 1.67 times in 2019 ( $T = 8.05$ ,  $p$ -value < 0.001) and was neutralized in 2021 ( $T = 0.94$ ,  $p$ -value = 0.357). This trend may be due to an increase in the presence of herbaceous vegetation over the years. At the air temperature there are no differences between the W-site and the C-site in 2016 ( $T = 1.88$ ,  $p$ -value = 0.071), in 2019 it is 2.90 °C warmer in the W-site compared to the C-site ( $T = 3.73$ ,  $p$ -value < 0.001), and in 2021 the



**Fig. 1. Microclimatic conditions within windthrow site (W) and closed-canopy site (C) in second (2016), fifth (2019) and seventh (2021) year after the windthrow.**

Note: Data represent the mean  $\pm$  SE ( $n \geq 30$ ). A two-tailed T-test is applied to estimate the difference between the sites each year. Asterisks denote statistically significant differences (\*\*\* $p$ -value < 0.001, \*\* $p$ -value < 0.01, \* $p$ -value < 0.05, n.s.:  $p$ -value > 0.05).

difference was almost the same – 2.89 °C ( $T = 2.56$ ,  $p$ -value = 0.016). No differences in CO<sub>2</sub> levels were observed between the two sites during any of the years of the experiment.

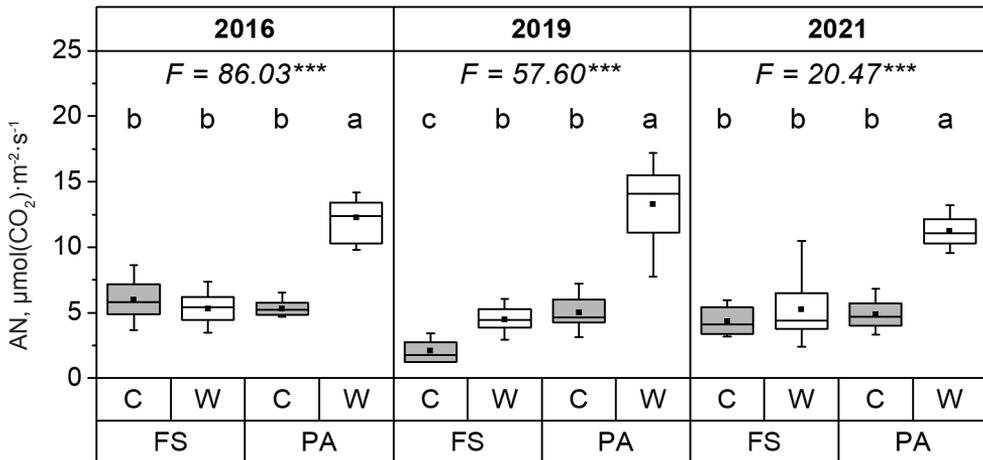
The effect of the increased solar radiation in the windthrow site is quickly apparent with the rise in the air temperature only two years after the windthrow, in contrast to the slighter decrease in air humidity. Still, as long as the  $T_{air}$  remained higher until the end of the study period, then the RH in the C-site is equal to that in the W-site in 2021, probably due to the newly appeared vegetation.

**Photosynthetic rate**

The net-photosynthetic rate in saturated light ( $A_N$ ) varied significantly between Species and Conditions interaction in ev-

ery experimental year. The common trend for all years was the higher  $A_N$  in PA-W, compared to the other variants. In 2016, it was 2.31, 2.32, and 2.05 times higher than that of PA-C, FS-W-site, and FS-C, respectively. In 2019 the differences increased – 2.65, 2.98, and 6.45 times, and in 2021 they were 2.31, 2.14, and 2.58 times, respectively (Fig. 2).

The maintenance of significantly higher photosynthesis of PA at the W-site shortly after the natural disturbance and keeping it high to the end of the experimental period is indicative of the rapid positive response of this species to the increased light after windthrow probably due to its pioneering character. Since early successional plants generally key in on disturbance, they stand astride pulses of available resources. Rapidly obtaining and using them before they subside and



**Fig. 2. Net-photosynthetic rate ( $A_N$ ) of *Fagus sylvatica* (FS) and *Prunus avium* (PA) in windthrow site (W) and closed-canopy site (C) in second (2016), fifth (2019), and seventh (2021) year after the windthrow.**

Note: The upper and the lower edges of each box indicate the 75th and 25th percentiles, respectively. The horizontal line within each box is the median, the square represents the mean, and the vertical bars indicate the 1.5 interquartile ranges. Two-way ANOVA (Factor A: Species and Factor B: Conditions) (Tukey test) is applied to estimate the difference between all the variants. Different letters denote statistically significant differences ( $p$ -value < 0.05).

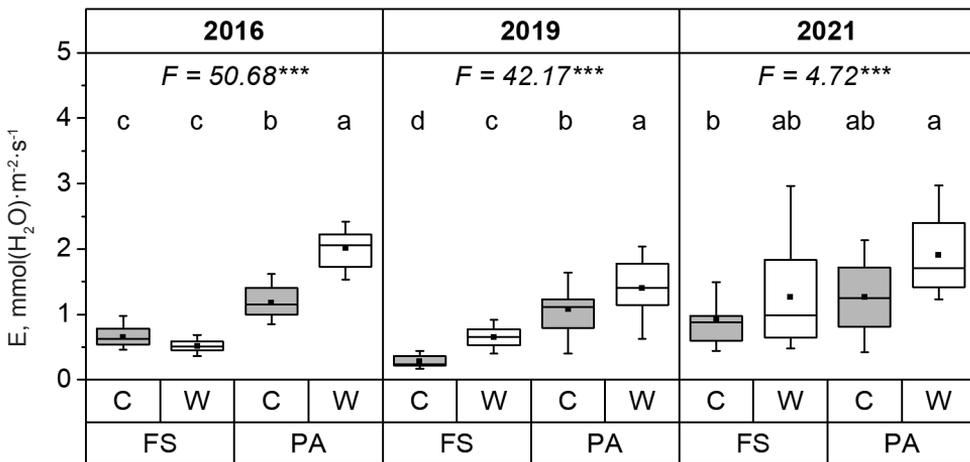
preventing competitors from obtaining them may be adaptive. The rapid increase in the growth rate of early successional trees when the canopy above them is removed (Marks 1974) is an example of this strategy. On the other hand, FS as a late-successional species reacts slower to the increased light relative to early successional PA, but it manages to take advantage of the higher irradiance and does not lower the  $A_N$  (except for slightly lower values for FS-C in 2019). This is a probable sign of a more conservative mechanism for adaptation to the sudden light.

### Transpiration rate

The transpiration rate ( $E$ ) varied significantly between Species and Conditions interaction for every year of the experiment. In addition to photosynthesis, PA-W

transpiration was also very intensive in 2016 and 2019, but in 2021 the differences with other variants decreased (Fig. 3).

The gradual increase in transpiration intensity in FS-W demonstrates the different potentials for adaptation to changed conditions. The authors (Bazzaz 1973, Berry 1975, Chabot 1977, Patterson et al. 1978) indicate that acclimation to the light environment that the plants experience during their growth seems to be more pronounced in the early than in the late-successional plants. In our experiment, PA reacts very quickly, and FS takes several years to begin to cool down its leaves adequately. Such slow adaptation is probably due to the need for a protective role of quickly settled pioneer vegetation in the herbaceous layer. Reynolds and Frochot (2003) state that young beech trees suddenly exposed to direct solar radiation and



**Fig. 3.** Transpiration rate ( $E$ ) of *Fagus sylvatica* (FS) and *Prunus avium* (PA) in windthrow site (W) and closed-canopy site (C) in second (2016), fifth (2019), and seventh (2021) year after a windthrow.

Note: The upper and the lower edges of each box indicate the 75th and 25th percentiles, respectively. The horizontal line within each box is the median, the square represents the mean, and the vertical bars indicate the 1.5 interquartile ranges. Two-way ANOVA (Factor A: Species and Factor B: Conditions) (Tukey test) is applied to estimate the difference between all the variants. Different letters denote statistically significant differences ( $p$ -value < 0.05).

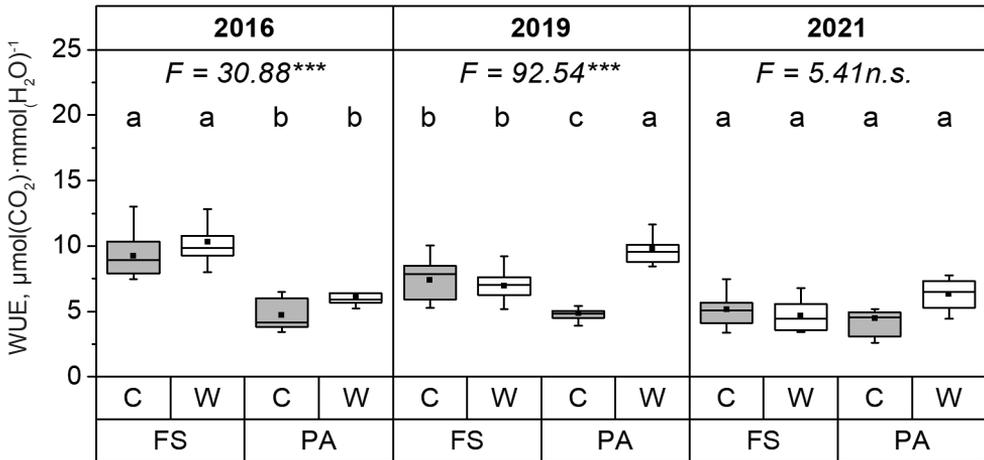
higher temperatures after removing parent stand shelter (e.g., wind disturbance) may close their stomata to prevent water deficit. In such a case, the gas exchange through stomata is limited, entailing the reduction of photosynthesis.

**Water-use efficiency**

The water-use efficiency (*WUE*) varied significantly in 2016 and 2019 but not in 2021 (Fig. 4).

The higher *WUE* in FS in 2016 was due not so much to high photosynthetic potential than to water savings. However, saving water (by reducing transpiration) could lead to increased leaf temperatures and might impose temperature stress. In the following experimental years, there was a downward trend in *WUE* in FS, which in 2021 even equaled that of PA. Bazzaz

and Boyer (1972) point out that usually, under optimal environmental conditions, *WUE* is lower in late than in early succession species. Under moderate stress conditions, a small decrease in stomatal conductivity can protect plants by improving water use efficiency. In shade-tolerant species, the stomata opening in response to increased light is significantly faster than in shade-intolerant species. Transpiration decreases more rapidly even with less negative water potential in shade-tolerant species than in shade-intolerant species (Bazzaz 1979). Thus, using their ability to utilize scattered solar radiation, shade-tolerant species can function better under the forest canopy than shade-intolerant ones but are less able to survive when water is scarce. At PA, *WUE*, except for the increase in PA-W in 2019, had a relatively constant value. Its equalization



**Fig. 4. Water-use efficiency (*WUE*) of *Fagus sylvatica* (FS) and *Prunus avium* (PA) in windthrow site (W) and closed-canopy site (C) in second (2016), fifth (2019), and seventh (2021) year after a windthrow.**

Note: The upper and the lower edges of each box indicate the 75th and 25th percentiles, respectively. The horizontal line within each box is the median, the square represents the mean, and the vertical bars indicate the 1.5 interquartile ranges. Two-way ANOVA (Factor A: Species and Factor B: Conditions) (Tukey test) is applied to estimate the difference between all the variants. Different letters denote statistically significant differences ( $p$ -value < 0.05).

in PA-W and PA-C in 2021 reflects the ongoing positive acclimatization of the species to changes in the environment.

### Total chlorophyll content

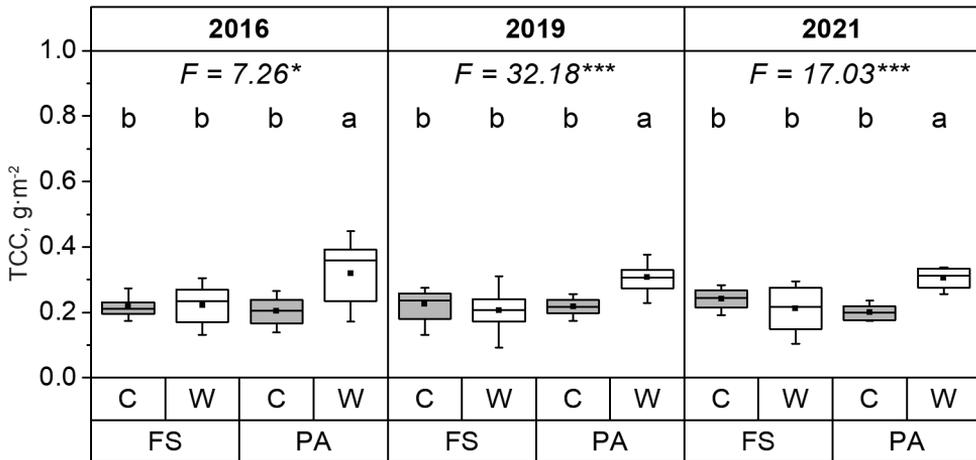
The total chlorophyll content (*TCC*) varied significantly between Species and Conditions interaction in every experimental year. The chlorophyll concentrations in FS leaves remained the same for the five-year period in W-site and C-site (Fig. 5).

A higher concentration of chlorophyll in the W-site than in C-site in PA results from the formation of a sun leaves, characterized by thicker leaf lamella. Although beech has a similar ability to form sun and shade leaves, probably due to the smaller number of chloroplasts in the sun leaves' mesophyll cells, such an increase of *TCC* was not observed in the W-site. Even after

a natural disturbance such as windthrow, the capacity to keep chlorophyll levels unchanged shows that FS has a wide tolerance for changes in light.

### Conclusion

This study indicates that the better physiological adaptation to changed microclimatic conditions after the windthrow disturbance of PA in comparison to FS is probably the main reason for the pioneer character of this species and rapid colonization of the territory. With its more economical water regime, PA increases its leaves' chlorophyll content after increasing the illumination. This allows it to take advantage of higher light and significantly increase its photosynthesis. The protective role of herbaceous plants, which in-



**Fig. 5.** Total chlorophyll content (*TCC*) of *Fagus sylvatica* (FS) and *Prunus avium* (PA) in windthrow site (W) and closed-canopy site (C) in second (2016), fifth (2019), and seventh (2021) year after a windthrow.

Note: The upper and the lower edges of each box indicate the 75th and 25th percentiles, respectively. The horizontal line within each box is the median, the square represents the mean, and the vertical bars indicate the 1.5 interquartile ranges. Two-way ANOVA (Factor A: Species and Factor B: Conditions) (Tukey test) is applied to estimate the difference between all the variants. Different letters denote statistically significant differences ( $p$ -value < 0.05).

vade a windthrow site, will enable FS to save the physiological activity and even increase physiological processes and parameters recently after disturbances. Such symbiosis between FS and pioneer grasses was also observed in other studies, which show that the appearance of mesophilic species in beech forests does not compete with FS saplings (Nedelin 1991). According to Stipcov and Ivanov (2013), the grass cover formed after disturbance does not interrupt but strengthens the beech undergrowth, which was confirmed, although at an early stage of FS development in our study.

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