

Photosystem II thermostability of apple tree leaves: effect of rootstock, crown shape and leaf topology

**Peter Ferus¹, Marián Brestič¹, Katarína Olšovská¹,
Anna Kubová²**

¹*Department of Plant Physiology, Slovak Agricultural University in Nitra,
Tr. A. Hlinku 2, 949 76 Nitra, Slovakia*

²*Experimental Orchard, Slovak Agricultural University in Nitra, Tr. A. Hlinku 2,
949 76 Nitra, Slovakia, e-mail: Marian.Brestic@uniag.sk*

Apple tree leaves usually experience extremely high summer temperatures, which might cause disturbances to their photosynthesis and negatively influence fruit loading and quality. In this respect, in apple trees of cv. 'Idared' we evaluated the effect of rootstock (very dwarfing M.9 and vigorous MM.104), crown shape (modified Slender spindle and modified Schlusser palmette) and leaf topology (leaves from the top of annual shoots, from the middle of the annual shoots and from short sprouts on the tree trunk) on the photosystem II (PS II) thermostability at the end of summer in 2006. For this purpose we analysed chlorophyll *a* fluorescence induction curves after exposure of leaf samples to 30 minutes of 42 °C. Neither rootstock types nor crown shapes caused any changes in the leaf PS II thermostability; however, significant differences in these characteristics were found in relation to leaf position in the apple tree crown. In comparison to leaves from annual shoots, which exhibited only moderate thermotolerance, a considerable increase was observed in leaves from short sprouts on the tree trunk. Measured high capacity of PS II thermotolerance is discussed in respect to plant polarity principles.

Key words: photosystem II thermotolerance, rootstock, crown shape, leaf topology, apple tree (*Malus domestica* Borkh.).

Introduction. Leaves are the main photosynthesizing plant organs providing assimilates for plant growth and fruit development. Leaves of apple tree (*Malus domestica* Borkh.) are developed from the leaf buds or combined floral-leaf buds. Passing exogenous dormancy, they expand to annual shoots with numerous leaf insertions. Intensive growth of annual shoots is timed particularly during spring and autumn. In summer their growth is usually decreased or almost stopped.

During vegetation period, developing leaves in the tree crown experience different endogenous and exogenous conditions determining their morphological, anatomical and biochemical characteristics, and hence their photosynthetic activity (Percy et al., 2005). In southern Slovakia, summer air temperatures usually reach 40 °C, which can have detrimental effects on photosynthesis (Salvucci and Crafs-Brandner, 2004) and, in a consequence, on fruit loading and quality. The final negative effect depends on leaf protective capacity on one side, and stress intensity and duration on the other side (Larcher, 2003).

Supraoptimal air temperature usually limits leaf photosynthesis through stomatal limitation of CO₂ uptake (Rahman, 2005; Cui et al., 2006), Rubisco deactivation (Law and Crafs-Brandner, 1999), thylakoid membrane injury (Liu and Huang, 2000), and photochemical PSII efficiency decline as a result of antenna detachment or impairment of electron transport chain components (Srivastava et al., 1997; Strasser, 2004). In the past two decades, a number of mechanisms alleviating these negative constraints was identified, including thermal dissipation (Bukhov et al., 1998); switch from the non-cyclic to cyclic electron transport (Bukhov et al., 1999); enhanced photorespiration (Sharkey, 2005); electron flux to oxygen (Mehler reaction) associated with up-regulated antioxidant system (Sairam et al., 2000) and chlororespiration (Wang et al., 2006); changes in the membrane composition in favour to saturated fatty acids (Larkindale and Huang, 2004) and accumulation of chemical (Kuznetsov et al., 1999) and molecular chaperones (Iba, 2002; Schroda, 2004).

Apple trees are composed of scion engrafted into a rootstock, which markedly regulates their growth (Webster, 1995). Tree crowns are formed into particular shapes in order to intercept more light and optimise fruit growth and ripening process. Both rootstock and crown shape influence hormonal composition of the scion (Webster, 1995; Tworkoski et al., 2006), and therefore can have significant effect on many physiological processes in leaves as well. Moreover, light conditions regulate leaves expansion and evoke different acclimation syndromes (Kull, 2002).

Very little is known about how these circumstances modify photosynthetic characteristics of apple tree leaves and what effect they have on photosynthetic processes in combination with elevated air temperature. In this work we focused on how rootstock differing in growth intensity, different crown shapes and leaf topology influence photosystem II (PS II) thermostability of leaves exposed to conditions of summer heat.

Object, methods and conditions. Plant material and cultivation. Apple trees (*Malus domestica* Borkh.) of cv. 'Idared', were cultivated in Experimental orchard of Slovak Agricultural University in Nitra, Slovakia, which is located on Nitra river alluvium (loamy-clayed soil substrate). The scion cultivar was engrafted into rootstock MM.104 (vigorous) and formed to modified Slender spindle or modified Schlusser palmette (20 years old trees), while apple trees engrafted into rootstock M.9 (very dwarfing) were formed to Slender spindle (8-years-old trees). Rows were oriented in north-southern direction, spaced 5 metres from each other, with in-row plant distance of 5 metres (older trees) and 1 meter (younger trees). Trees were approximately 3 (older trees) and 2 metres high (younger trees), and their crown diameter/width was 2.5 m (older trees, modified Slender spindle), 1.25 m (older trees, modified Schlusser palmette) and 1 m (younger trees, Slender spindle), respectively.

In autumn, phosphoric and potassium fertilization combined with cultivation was applied. During the vegetation period, trees were fertilized by nitrogen and for prevention treated against powdery mildew (*Podosphaera leucotricha*), apple scab (*Venturia inaequalis*) and herbivores. Weeds were regulated mechanically.

In the fruit growing and ripening growth stage (beginning of September), young

5th leaves of east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the tree trunks were collected in the mornings of three consecutive sunny days, transferred to laboratory, acclimated to darkness for 30 minutes and subjected to photosystem II (PS II) thermostability test.

Photosystem II thermostability test. Samples of leaf halves were enclosed in the test tubes and submerged into water bath of 42 °C for 30 minutes in the darkness. Before and after exposure of samples to high temperature, chlorophyll *a* fluorescence induction kinetics of the samples (12 leaves per treatment, 5 replicates per a leaf) were determined by Handy-PEA, Hansatech Instruments Ltd., UK. Their normalizations enabled to determine relative variable fluorescence at J and I step (V_j and V_i), ratio of fluorescence at K and J step of the induction curves (F_k/F_j) and maximal photochemical efficiency of PS II (F_v/F_m). After that, the JIP test (BioLyzer 4HP v. 3.06 software, Ronald Rodriguez) was applied to the fluorescence induction curves, which revealed further characteristics of the PS II bioenergetic state (Strasser et al., 2000; Strasser et al., 2004), such as maximal quantum yield of primary photochemistry (Φ_{p_0}), exciton transfer efficiency to electron transport chain (Ψ_o), electron transport yield (Φ_{E_o}) and thermal dissipation yield (Φ_{D_o}).

Determination of photosynthetic pigments concentration. For this purpose, second halves of leaf samples were utilized. Segments of the samples were homogenised in the presence of sea sand, $MgCO_3$ and 100 % acetone. After acetone vaporisation the homogenates were transferred into 80 % acetone and after centrifugation for 2 minutes at 2 500 rpm light absorption of the solutions was read at 470, 647 and 663 nm using spectrophotometer Jenway, UK. The pigment concentrations per leaf area unit were calculated according to Lichtenthaler (1987).

During the summer months, maximal daily air temperatures and daily rainfall in the experimental orchard was recorded by automatic agrometeorological station.

Statistical data analysis (ANOVA) was accomplished using application Statgraphics Plus v. 4.0.

Results. Photosynthetic apparatus of apple trees before high temperature treatment. Chlorophyll *a* fluorescence induction curves of leaves from modified Slender spindle apple trees grafted into vigorous rootstock MM.104 (Fig. 1) showed very similar course at the beginning (O step). At J step they started to differ significantly with much more steeper fluorescence rise to I step in the leaves of south-oriented short sprouts on the trunk (inner-crown leaves) followed by slighter rise to P step. Fluorescence transients from J to P step in the 5th and middle leaves of east-oriented annual shoots were almost parallel. However, the latter gained significantly lower values.

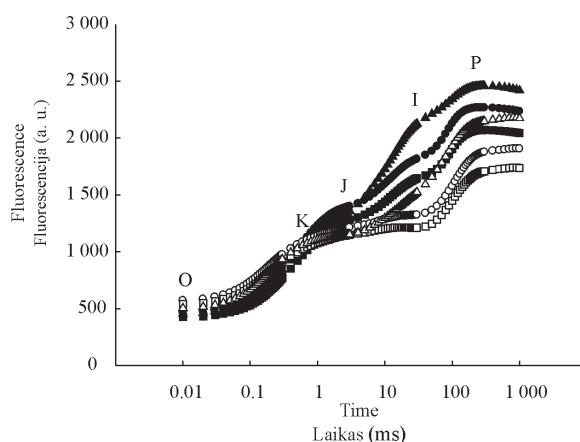


Fig. 1. Chlorophyll *a* fluorescence induction curves (OJIPs) in control (full symbols) and high temperature (30 min of 42 °C in the darkness) treated (empty symbols) leaves from apple trees of cultivar ‘Idared’ formed to modified Slender spindle and engrafted into vigorous rootstock MM.104: 5th leaves of east-oriented annual shoots (circles), leaves of the middle part of the same shoots (squares) and leaves of the south-oriented short sprouts on the tree trunks (triangles).

1 pav. Chlorofilo *a* fluorescencijos indukcijos kreivės nepaveiktuose (užtušuoti simboliai) ir aukšta temperatūra (42 °C 30 min tamsoje) paveiktuose (tuščiaviduriai simboliai) modifikuotos laibosios verpstės formos ‘Idared’ veislės obelių su MM.104 poskiepiu lapuose. Imti penkti lapai nuo į rytus orientuoto metūglio (rutuliukai), lapai nuo vidurinės šakų dalies (kvadratėliai) ir lapai nuo į šiaurę orientuotų vaisinių šakučių (trikampėliai).

Parameters derived from fluorescence induction curves, such as basal fluorescence (F_0) and relative variable fluorescence at the J and I step of the induction curves (V_j and V_i) (Table 1) also confirm this tendency. On the other hand, maximal photochemical efficiency of PS II (F_v/F_m) did not show statistically significant difference between the leaves. Fluorescence at K versus J step of the induction curves (F_k/F_j) was slightly enhanced in the inner-crown leaves. JIP test applied to the fluorescence induction curves revealed significantly higher exciton transfer efficiency to electron transport chain (Ψ_0) and electron transport yield (Φ_{E_0}) in the inner-crown leaves, but they had no effect on maximal quantum yield of primary photochemistry (Φ_{P_0}) (Fig. 2). Thermal dissipation yield (Φ_{D_0}) also showed balanced values in each leaf position.

Table 1. Parameters derived from chlorophyll *a* fluorescence induction curves measured in 5th leaves of east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the apple tree trunks (inner-crown), of cultivar ‘Idared’ before the high temperature treatment (30 min at 42 °C in the darkness): F_o – basal fluorescence, V_j and V_i – relative variable fluorescence at J and I step of the fluorescence induction curve, F_k/F_j – ratio of chlorophyll *a* fluorescence at K versus J step of the induction curve, and F_v/F_m – maximal photochemical efficiency of PS II. Letters indicate statistically significant difference at $P = 0.01$.

1 lentelė. Išvestiniai parametrai iš chlorofilo *a* fluorescencijos indukcijos kreivių, matuotų ‘Idared’ veislės obelių penktuose lapuose nuo į rytus orientuoto metūglio, lapuose nuo vidurinės šakų dalies ir lapuose nuo į pietus orientuotų vaisinių šakučių. Analizės atliktos prieš aukštos temperatūros poveikį (42 °C 30 min tamsoje). F_o – bazinė fluorescencija, V_j ir V_i – J ir I fluorescencijos indukcijos kreivės žingsniuose santykinai kintanti fluorescencija, F_k/F_j – chlorofilo *a* fluorescencijos santykis tarp K ir J žingsnių, F_v/F_m – maksimalus fotocheminis PS II efektyvumas. Raidės žymi statistiškai patikimus skirtumus, kai $P = 0,01$.

Leaf Lapas	F_o	V_j	V_i	F_k/F_j	F_v/F_m
MM.104, modified Slender spindle MM.104, modifikuota verpstė					
Fifth leaf Penktas lapas	434 ± 38 <i>a</i>	0.487 ± 0.040 <i>b</i>	0.742 ± 0.021 <i>a</i>	0.628 ± 0.024 <i>ab</i>	0.808 ± 0.019 <i>a</i>
Middle leaf Vidurinis lapas	401 ± 34 <i>a</i>	0.490 ± 0.061 <i>b</i>	0.736 ± 0.022 <i>a</i>	0.618 ± 0.022 <i>a</i>	0.805 ± 0.026 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	426 ± 25 <i>a</i>	0.414 ± 0.043 <i>a</i>	0.830 ± 0.016 <i>b</i>	0.642 ± 0.011 <i>b</i>	0.826 ± 0.008 <i>a</i>
M.9, Slender spindle M.9, verpstė					
Fifth leaf Penktas lapas	449 ± 33 <i>b</i>	0.512 ± 0.038 <i>b</i>	0.738 ± 0.019 <i>a</i>	0.630 ± 0.028 <i>a</i>	0.789 ± 0.021 <i>a</i>
Middle leaf Vidurinis lapas	365 ± 43 <i>a</i>	0.451 ± 0.062 <i>ab</i>	0.729 ± 0.017 <i>a</i>	0.615 ± 0.025 <i>a</i>	0.805 ± 0.029 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	384 ± 19 <i>a</i>	0.413 ± 0.052 <i>a</i>	0.792 ± 0.024 <i>b</i>	0.619 ± 0.010 <i>a</i>	0.833 ± 0.008 <i>b</i>
MM.104, modified Schlösser palmette MM.104, modifikuotas Schlösser palmette					
Fifth leaf Penktas lapas	459 ± 31 <i>b</i>	0.479 ± 0.031 <i>a</i>	0.743 ± 0.015 <i>a</i>	0.642 ± 0.025 <i>ab</i>	0.796 ± 0.019 <i>a</i>
Middle leaf Vidurinis lapas	396 ± 38 <i>a</i>	0.452 ± 0.066 <i>a</i>	0.722 ± 0.030 <i>a</i>	0.630 ± 0.026 <i>a</i>	0.801 ± 0.028 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	468 ± 31 <i>b</i>	0.462 ± 0.035 <i>a</i>	0.839 ± 0.021 <i>b</i>	0.669 ± 0.024 <i>b</i>	0.810 ± 0.017 <i>a</i>

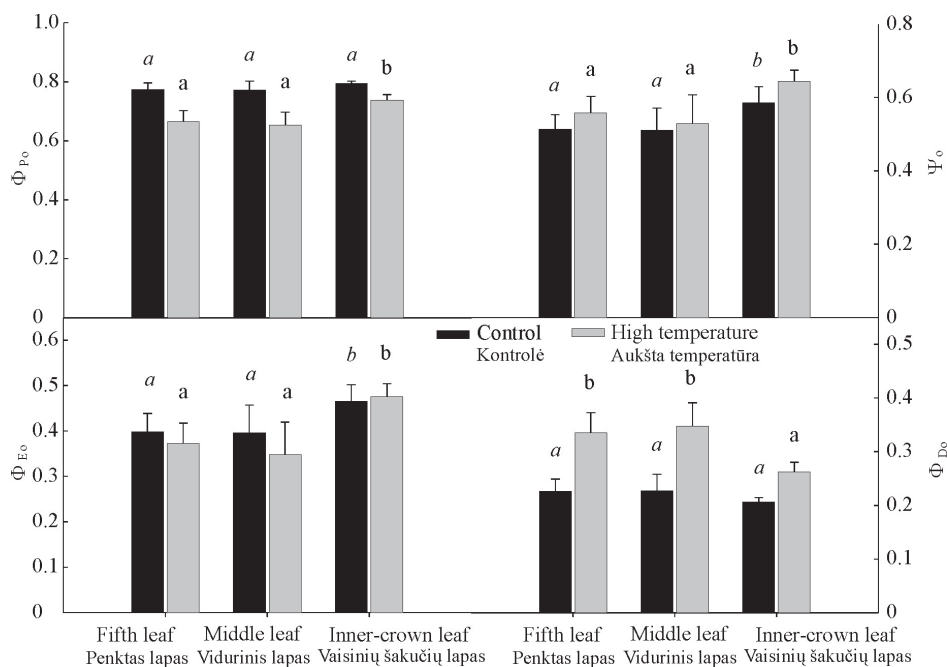


Fig. 2. Parameters derived from chlorophyll *a* fluorescence induction curves measured in the 5th leaves of east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the tree trunks (inner-crown) from apple trees, of cultivar 'Idared', formed to modified Slender spindle and engrafted into vigorous rootstock MM.104, before and after the high temperature treatment (30 min of 42 °C in the darkness): Φ_{p_0} – maximal quantum yield of primary photochemistry, Ψ_0 – exciton transfer efficiency to electron transport chain, Φ_{E_0} – electron transport yield, Φ_{D_0} – thermal dissipation yield. Letters indicate statistically significant difference at $P = 0.01$: italic – before, and normal – after the high temperature treatment.

2 pav. Išvestiniai parametrai iš chlorofilo *a* fluorescencijos indukcijos kreivių, matuotų modifikuotos laibosios verpstės formos 'Idared' veislės obelų su MM.104 poskiepiu penktuose lapuose nuo į rytus orientuoto metūglio, lapuose nuo vidurinės šakų dalies ir lapuose nuo į pietus orientuotų vaisinių šakučių.

Analizės atliktos prieš ir po temperatūros poveikio (42 °C 30 min tamsoje). Φ_{p_0} – maksimali pirminės fotochemijos kvantų išeiga, Ψ_0 – eksitono perdavimo į elektronų transporto grandinę efektyvumas, Φ_{E_0} – elektronų transporto išeiga, Φ_{D_0} – šilumos sklaidos išeiga.

Raidės žymi statistiškai patikimus skirtumus kai $P = 0,01$, pasvirasis šifras – prieš, normalus – po temperatūros poveikio.

In Slender spindle apple trees engrafted into very dwarfing rootstock M.9, the middle leaves on annual shoots and the inner-crown leaves displayed lower fluorescence values at J step of the fluorescence induction curves, followed by generally slower fluorescence increase to P step in comparison to leaves of apple trees engrafted into rootstock MM.104 (Fig. 3).

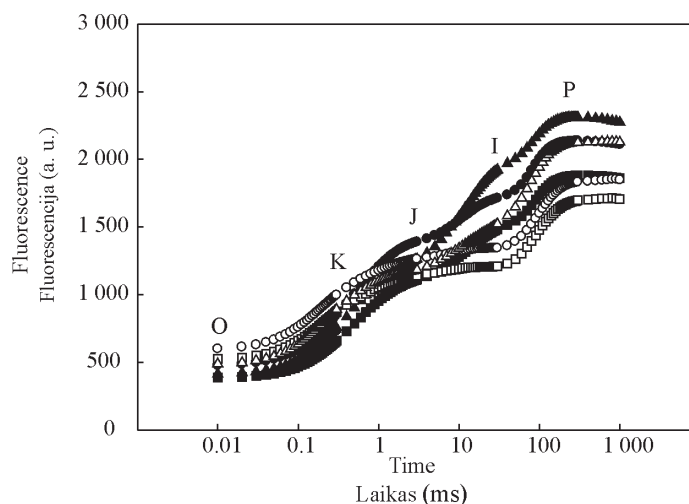


Fig. 3. Chlorophyll *a* fluorescence induction curves (OJIPs) in control (full symbols) and high temperature (30 min of 42 °C in the darkness) treated (empty symbols) leaves from apple trees of cultivar ‘Idared’, formed to Slender spindle and engrafted into very dwarfing rootstock M.9: 5th leaves of east-oriented annual shoots (circles), leaves of the middle part of the same shoot (squares) and leaves of the south-oriented short sprouts on the tree trunks (triangles).

3 pav. Chlorofilo *a* fluorescencijos indukcijos kreivės nepaveiktuose (užtušuoti simboliai) ir aukšta temperatūra (42 °C 30 min. tamsoje) paveiktuose (tuščiaviduriai simboliai) modifikuotos laibosios verpstės formos ‘Idared’ veislės obelų su M.9 poskiepiu lapuose. Imti penkti lapai nuo į rytus orientuoto metūglio (rutuliukai), lapai nuo vidurinės šakų dalies (kvadratėliai) ir lapai nuo į pietus orientuotų vaisinių šakučių (trikampėliai).

In these leaves F_0 reached markedly lower values than in the 5th leaves of annual shoots (Table 1). The 5th leaves also dominated in V_j , while F_k/F_j did not change with leaf position. F_v/F_m was the highest in the inner-crown leaves. Significant differences among the JIP test parameters were only obtained in the 5th leaves of annual shoots and inner-crown leaves (Fig. 4). The inner-crown leaves reached higher Φ_{P_0} , Ψ_o , Φ_{E_0} , and lower Φ_{D_0} than the 5th ones.

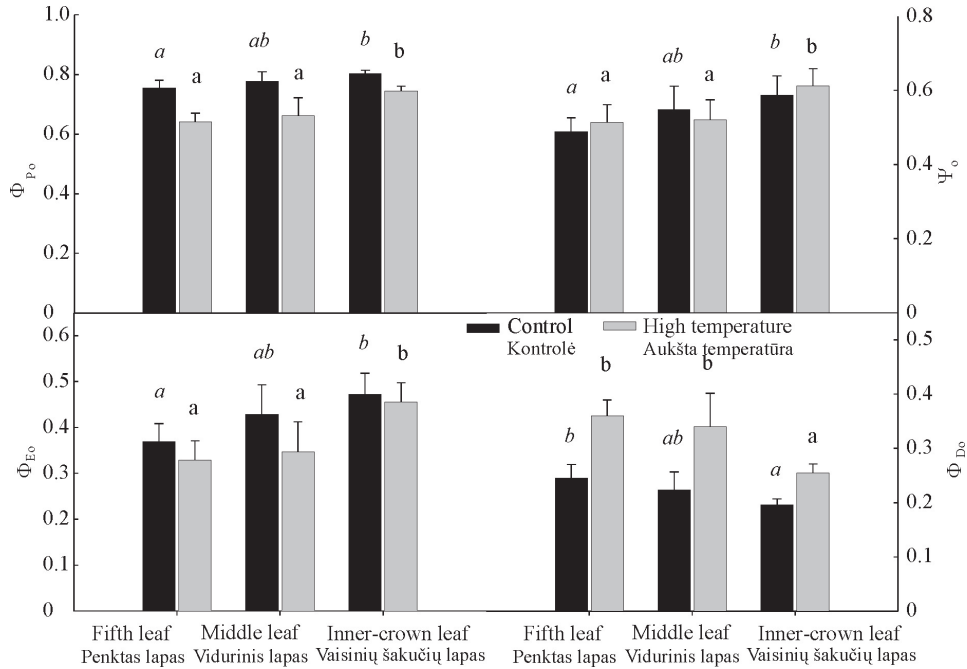


Fig. 4. Parameters derived from chlorophyll *a* fluorescence induction curves measured in the 5th leaves of east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the tree trunks (inner-crown) from apple trees of cultivar ‘Idared’, formed to Slender spindle and engrafted into very dwarfing rootstock M.9, before and after the high temperature treatment (30 min of 42 °C in the darkness):

Φ_{p_0} – maximal quantum yield of primary photochemistry,

Ψ_0 – exciton transfer efficiency to electron transport chain,

Φ_{E_0} – electron transport yield,

Φ_{D_0} – thermal dissipation yield.

Letters indicate statistically significant difference at $P = 0.01$:

italic – before, and normal – after the high temperature treatment.

4 pav. Išvestiniai parametrai iš chlorofilo *a* fluorescencijos indukcijos kreivių, matuotų modifikuotos laibosios verpstės formos ‘Idared’ veislės obelų su M.9 poskiepiu penktuose lapuose nuo į rytus orientuoto metūglio,

lapuose nuo vidurinės šakų dalies ir lapuose nuo į pietus orientuotų vaisinių šakučių. Analizės atliktos prieš ir po temperatūros poveikio (42 °C 30 min tamsoje).

Φ_{p_0} – maksimali pirminės fotochemijos kvantų išeiga,

Ψ_0 – eksitono perdavimo į elektronų transporto grandinę efektyvumas,

Φ_{E_0} – elektronų transporto išeiga,

Φ_{D_0} – šilumos sklaidos išeiga. Raidės žymi statistiškai patikimus skirtumus, kai $P = 0,01$, pasvirasis šifras – prieš, normalus – po temperatūros poveikio.

Except of markedly lower fluorescence values at O and J step of the fluorescence induction curves in the middle leaves of annual shoots, leaves from Schlösser palmette apple trees engrafted into vigorous rootstock MM.104 (Fig. 5) exhibited very similar fluorescence transients to those from modified Slender spindle apple trees engrafted into the same rootstock.

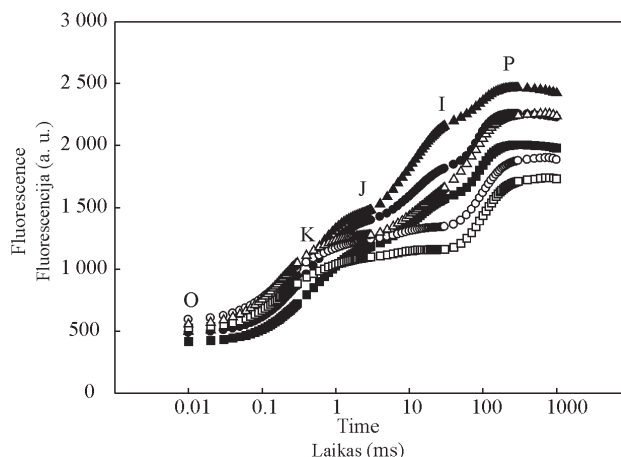


Fig. 5. Chlorophyll *a* fluorescence induction curves (OJIPs) in control (full symbols) and high temperature (30 min of 42 °C in the darkness) treated (empty symbols) leaves from apple trees of cultivar ‘Idared’, formed to modified Schlösser palmette and engrafted into vigorous rootstock MM.104: 5th leaves of east-oriented annual shoots (circles), leaves of the middle part of the same shoot (squares) and leaves of the south-oriented short sprouts on the tree trunks (triangles).

5 pav. Chlorofilo *a* fluorescencijos indukcijos kreivės nepaveiktuose (užtušuoti simboliai) ir aukšta temperatūra (42 °C 30 min. tamsoje) paveiktuose (tuščiaviduriai simboliai) modifikuotos Schlösser palmetės formos ‘Idared’ veislės obelių su MM.104 poskiepiu lapuose. Imti penkti lapai nuo į rytus orientuoto metūglio (rutuliukai), lapai nuo vidurinės šakų dalies (kvadratėliai) ir lapai nuo į šiaurę orientuotų vaisinių šakučių (trikampėliai).

Consequently, F_o was reduced in the middle leaves of annual shoots, and V_i (Table 1) with JIP test parameters Y_o and F_{Eo} revealed no difference between leaf positions (Fig. 6).

Photosynthetic pigments concentration and chl./car. ratio exhibited no significant difference between leaf positions in the modified Slender spindle apple trees engrafted into rootstock MM.104 (Table 2). However, chlorophyll *a/b* ratio of inner-crown leaves was the lowest among all leaf positions.

Despite of significant reduction of chlorophyll *a* concentration in the inner-crown leaves of the Slender spindle apple trees engrafted into rootstock M.9 (this rootstock – crown shape combination exhibited the highest chlorophyll *a* concentrations), leaf position did not influence the chlorophyll *a/b* ratio. Chlorophyll *b* and carotenoids concentrations and chl./car. ratio were also very similar.

Among rootstock – crown shape combinations, markedly lower chlorophyll *a*, *b* and carotenoids concentrations accompanied by decrease of chlorophyll *a/b* ratio

in the inner-crown leaves were only observed in modified Schlösser palmette apple trees on the rootstock MM.104. Besides, 5th and the middle leaves on annual shoots of these apple trees dominated in carotenoid concentration.

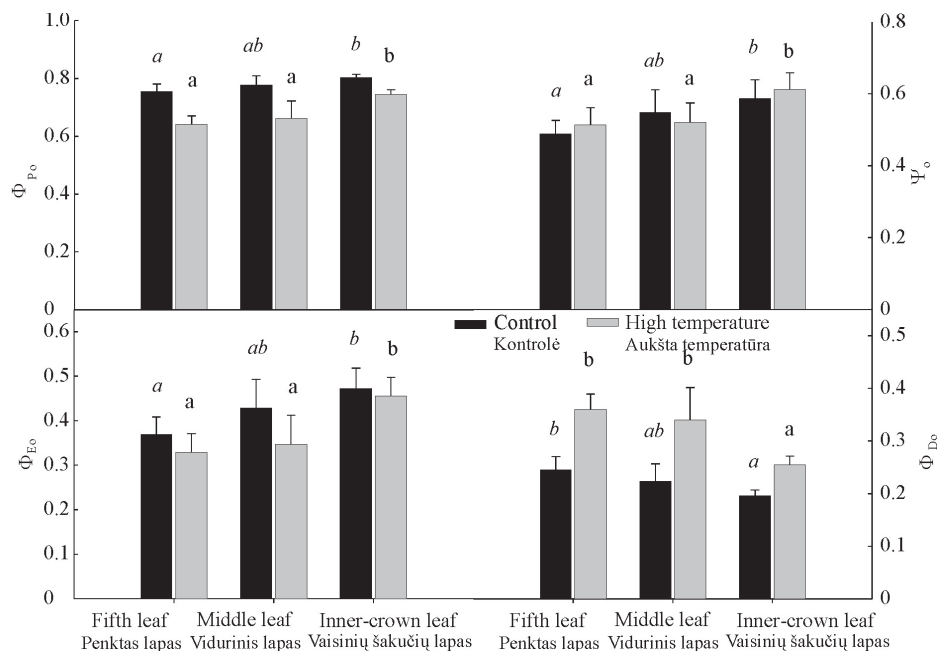


Fig. 6. Parameters derived from chlorophyll *a* fluorescence induction curves measured in the 5th leaves of east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the tree trunks (inner-crown) from apple trees, of cultivar 'Idared', formed to modified Schlösser palmette and engrafted into vigorous rootstock MM.104, before and after the high temperature treatment (30 min of 42 °C in the darkness):

Φ_{p_0} – maximal quantum yield of primary photochemistry,

Ψ_o – exciton transfer efficiency to electron transport chain,

Φ_{E_o} – electron transport yield, Φ_{D_o} – thermal dissipation yield.

Letters indicate statistically significant difference at $P = 0.01$:

italic – before, and normal font – after the high temperature treatment.

6 pav. Išvestiniai parametrai iš chlorofilo *a* fluorescencijos indukcijos kreivių, matuotų modifikuotos Schlösser palmetės formos 'Idared' veislės obelių su MM.104 poskiepiu penktuose lapuose nuo į rytus orientuoto metūglio, lapuose nuo vidurinės šakų dalies ir lapuose nuo į pietus orientuotų vaisinių šakučių. Analizės atliktos prieš ir po temperatūros poveikio (42 °C 30 min tamsoje).

Φ_{p_0} – maksimali pirminės fotochemijos kvantų išeiga,

Ψ_o – eksitono perdavimo į elektronų transporto grandinę efektyvumas,

Φ_{E_o} – elektronų transporto išeiga, Φ_{D_o} – šilumos sklaidos išeiga.

Raidės žymi statistiškai patikimus skirtumus, kai $P = 0,01$, pasvirasis šifras – prieš, normalus – po temperatūros poveikio.

Table 2. Photosynthetic pigment concentration (mg m^{-2}) in the 5th leaves on east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the tree trunks (inner-crown) from apple trees, of cultivar ‘Idared’, with different rootstock and crown shape. Letters indicate statistically significant difference at $P = 0.01$.

2 lentelė. Photosintezės pigmentų koncentracija (mg m^{-2}) skirtingos formos ‘Idared’ veislės obelių su skirtingais poskiepiais penktuose lapuose nuo į rytus orientuoto metūglio, lapuose nuo vidurinės šakų dalies ir lapuose nuo į pietus orientuotų vaisinių šakučių. Raidės žymi statistiškai patikimus skirtumus kai $P = 0,01$.

Leaf Lapas	Chlorophyll <i>a</i> Chlorofilas <i>a</i>	Chlorophyll <i>b</i> Chlorofilas <i>b</i>	Carotenoids Karotenoidai	Chlorophyll <i>a/b</i> Chlorofilai <i>a/b</i>	Chlorophylls / carotenoids Chlorofilai / karotenoidai
MM.104, modified Slender spindle MM.104, modifikuota verpstė					
Fifth leaf Penktas lapas	618.28 ± 47.96 <i>a</i>	225.44 ± 36.81 <i>a</i>	277.75 ± 63.07 <i>a</i>	2.79 ± 0.35 <i>b</i>	3.21 ± 0.87 <i>a</i>
Middle leaf Vidurinis lapas	632.21 ± 87.40 <i>a</i>	237.58 ± 34.62 <i>a</i>	322.86 ± 128.17 <i>a</i>	2.67 ± 0.26 <i>ab</i>	3.06 ± 1.15 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	554.05 ± 76.88 <i>a</i>	239.19 ± 42.94 <i>a</i>	306.46 ± 111.98 <i>a</i>	2.35 ± 0.31 <i>a</i>	2.91 ± 1.07 <i>a</i>
M.9, Slender spindle M.9, verpstė					
Fifth leaf Penktas lapas	720.77 ± 163.76 <i>b</i>	287.90 ± 88.44 <i>a</i>	353.89 ± 110.63 <i>a</i>	2.56 ± 0.22 <i>a</i>	3.03 ± 0.82 <i>a</i>
Middle leaf Vidurinis lapas	714.42 ± 48.32 <i>b</i>	276.23 ± 46.44 <i>a</i>	401.58 ± 54.08 <i>a</i>	2.65 ± 0.47 <i>a</i>	2.51 ± 0.38 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	563.97 ± 60.40 <i>a</i>	239.33 ± 32.00 <i>a</i>	326.73 ± 29.12 <i>a</i>	2.37 ± 0.14 <i>a</i>	2.49 ± 0.44 <i>a</i>
MM.104, modified Schlösser palmette MM.104, modifikuotas Schlösser palmette					
Fifth leaf Penktas lapas	630.44 ± 0.96 <i>b</i>	256.25 ± 30.76 <i>b</i>	429.65 ± 102.37 <i>ab</i>	2.47 ± 0.15 <i>b</i>	2.17 ± 0.57 <i>a</i>
Middle leaf Vidurinis lapas	603.76 ± 9.43 <i>b</i>	242.09 ± 30.25 <i>b</i>	440.26 ± 133.51 <i>b</i>	2.50 ± 0.17 <i>b</i>	2.14 ± 0.84 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	411.83 ± 3.95 <i>a</i>	192.25 ± 21.58 <i>a</i>	305.72 ± 52.14 <i>a</i>	2.14 ± 0.06 <i>a</i>	2.02 ± 0.37 <i>a</i>

Photosystem II activity in apple tree leaves treated with high temperature. Thirty minutes treatment by temperature of 42 °C in the darkness caused a significant increase of F_o , F_k/F_j and Φ_{D_o} , and decrease of V_i , F_v/F_m and Φ_{P_o} in all rootstock-crown shape-leaf position combinations (Table 3). Inner-crown leaves of apple trees on rootstock MM.104 also showed lower V_i and higher Ψ_o .

In comparison to control measurements, fluorescence induction curves of leaves from modified Slender spindle apple trees engrafted into rootstock MM.104 exhibited higher fluorescence at the O step, reduced fluorescence at the J and particularly I step, followed by markedly lower fluorescence values at the P step (Fig. 1). Parallel to these changes, relations between fluorescence transients of leaves from different positions stayed relatively stable.

Table 3. Evaluation of statistical difference of parameters derived from chlorophyll *a* fluorescence induction curves between control and high temperature (30 min at 42 °C in the darkness) treated apple tree leaves. F_o – basal fluorescence, V_j and V_i – relative variable fluorescence at J and I step of the fluorescence induction curve, F_k/F_j – ratio of fluorescence at K versus J step of the fluorescence induction curve, F_v/F_m – maximal photochemical efficiency of PS II, Φ_{p_o} – maximal quantum yield of primary photochemistry, Ψ_o – exciton transfer efficiency to electron transport chain, Φ_{E_o} – electron transport yield, Φ_{D_o} – thermal dissipation yield. Double asterisk indicates on statistically significant difference at $P = 0.01$, asterisks indicates on statistically significant difference at $P = 0.05$ and n. s. – non-significant difference.

3 lentelė. Išvestinių parametrų iš chlorofilo *a* fluorescencijos indukcijos kreivių statistinių skirtumų tarp nepaveiktų ir aukšta temperatūra (42 °C 30 min. tamsoje) paveiktų vaismedžių įvertinimas. F_o – bazinė fluorescencija, V_j ir V_i – J ir I fluorescencijos indukcijos kreivės žingsniuose santykinai kintanti fluorescencija, F_k/F_j – chlorofilo *a* fluorescencijos santykis tarp K ir J žingsnių, F_v/F_m – maksimalus fotocheminis PS II efektyvumas. Φ_{p_o} – maksimali pirminės fotochemijos kvantų išeiga, Ψ_o – eksitono perdavimo į elektronų transporto grandinę efektyvumas, Φ_{E_o} – elektronų transporto išeiga, Φ_{D_o} – šilumos sklaidos išeiga. Dvi žvaigždutės žymi statistiškai patikimus skirtumus, kai $P = 0,01$, žvaigždutė žymi statistiškai patikimus skirtumus kai $P = 0,05$.

Leaf Lapas	F_o	V_j	V_i	F_k/F_j	F_v/F_m	Φ_{p_o}	Ψ_o	Φ_{E_o}	Φ_{D_o}
MM.104, modified Slender spindle									
MM.104, modifikuota verpstė									
Fifth leaf Penktas lapas	**	*	**	**	**	**	*	n. s.	**
Middle leaf Vidurinis lapas	**	n. s.	**	**	**	**	n. s.	n. s.	**
Inner-crown leaf Vaisinių šakučių lapas	**	**	**	**	**	**	**	n. s.	**
M.9, Slender spindle									
M.9, verpstė									
Fifth leaf Penktas lapas	**	n. s.	**	**	**	**	n. s.	*	**
Middle leaf Vidurinis lapas	**	n. s.	**	**	**	**	n. s.	*	**
Inner-crown leaf Vaisinių šakučių lapas	**	n. s.	**	**	**	**	n. s.	n. s.	**
MM.104, modified Schlösser palmette									
MM.104, modifikuotas Schlösser palmette									
Fifth leaf Penktas lapas	**	n. s.	**	**	**	**	n. s.	*	**
Middle leaf Vidurinis lapas	**	n. s.	**	**	**	**	n. s.	n. s.	**
Inner-crown leaf Vaisinių šakučių lapas	**	**	**	**	**	**	**	n. s.	**

From them the lowest F_o and V_j values, and the highest F_v/F_m of inner-crown leaves were derived (Table 4). Leaf positions did not influence values of V_i and F_k/F_j . These results were reflected in JIP test parameters: the inner-crown leaves showed the highest Ψ_o , Φ_{E_o} and Φ_{p_o} , but the lowest Φ_{D_o} (Fig. 2).

Table 4. Parameters derived from chlorophyll *a* fluorescence induction curves measured in 5th leaves of east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the apple tree trunks (inner-crown), after the high temperature treatment (30 min at 42 °C in the dark): F_o – basal fluorescence, V_j and V_i – relative variable fluorescence at J and I step of the fluorescence induction curve, F_k/F_j – ratio of chlorophyll *a* fluorescence at K versus J step of the induction curve, and F_v/F_m – maximal photochemical efficiency of PS II. Letters indicate statistically significant difference at $P = 0.01$.

4 lentelė. Išvestiniai parametrai iš chlorofilo *a* fluorescencijos indukcijos kreivių, matuotų 'Idared' veislės obelių penktuose lapuose nuo rytus orientuoto metūglio, lapuose nuo vidurinės šakų dalies ir lapuose nuo pietus orientuotų vaisinių šakučių. Analizės atliktos po aukštos temperatūros poveikio (42 °C 30 min. tamsoje). F_o – bazinė fluorescencija, V_j ir V_i – J ir I fluorescencijos indukcijos kreivės žingsniuose santykinai kintanti fluorescencija, F_k/F_j – chlorofilo *a* fluorescencijos santykis tarp K ir J žingsnių, F_v/F_m – maksimalus fotocheminis PS II efektyvumas. Raidės žymi statistiškai patikimus skirtumus kai $P = 0,01$.

Leaf Lapas	F_o	V_j	V_i	F_k/F_j	F_v/F_m
MM.104, modified Slender spindle MM.104, modifikuota verpstė					
Fifth leaf Penktas lapas	549 ± 62 <i>b</i>	0.441 ± 0.045 <i>b</i>	0.541 ± 0.065 <i>a</i>	0.817 ± 0.037 <i>a</i>	0.711 ± 0.033 <i>a</i>
Middle leaf Vidurinis lapas	521 ± 53 <i>ab</i>	0.471 ± 0.078 <i>b</i>	0.539 ± 0.063 <i>a</i>	0.807 ± 0.024 <i>a</i>	0.700 ± 0.039 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	475 ± 23 <i>a</i>	0.356 ± 0.031 <i>a</i>	0.593 ± 0.045 <i>a</i>	0.819 ± 0.025 <i>a</i>	0.781 ± 0.016 <i>b</i>
M.9, Slender spindle M.9, verpstė					
Fifth leaf Penktas lapas	580 ± 50 <i>b</i>	0.487 ± 0.048 <i>b</i>	0.573 ± 0.052 <i>a</i>	0.803 ± 0.025 <i>a</i>	0.686 ± 0.028 <i>a</i>
Middle leaf Vidurinis lapas	506 ± 86 <i>ab</i>	0.479 ± 0.053 <i>b</i>	0.555 ± 0.021 <i>a</i>	0.703 ± 0.057 <i>a</i>	0.779 ± 0.040 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	458 ± 24 <i>a</i>	0.389 ± 0.047 <i>a</i>	0.616 ± 0.073 <i>a</i>	0.769 ± 0.025 <i>a</i>	0.785 ± 0.014 <i>b</i>
MM.104, modified Schlösser palmette MM.104, modifikuotas Schlösser palmette					
Fifth leaf Penktas lapas	575 ± 51 <i>b</i>	0.455 ± 0.063 <i>b</i>	0.552 ± 0.074 <i>a</i>	0.822 ± 0.031 <i>a</i>	0.697 ± 0.032 <i>a</i>
Middle leaf Vidurinis lapas	506 ± 48 <i>a</i>	0.438 ± 0.063 <i>ab</i>	0.504 ± 0.075 <i>a</i>	0.817 ± 0.037 <i>a</i>	0.709 ± 0.019 <i>a</i>
Inner-crown leaf Vaisinių šakučių lapas	527 ± 42 <i>a</i>	0.390 ± 0.035 <i>a</i>	0.632 ± 0.048 <i>b</i>	0.832 ± 0.034 <i>a</i>	0.765 ± 0.027 <i>b</i>

Fluorescence induction curves in the middle leaves of annual shoots and inner-crown leaves from Slender spindle apple trees engrafted into rootstock M.9 did not exhibit lower fluorescence values at the J step than before high temperature treatment (Fig. 3). Except of this difference, fluorescence transients of these as well as the 5 th leaves resembled those from modified Slender spindle apple trees engrafted into rootstock MM.104. Also the parameters derived from fluorescence induction curves showed the same tendency as in these apple trees (Table 4, Fig. 4).

Comparison of fluorescence induction curves in leaves from modified Schlösser palmette apple trees engrafted into rootstock MM.104 before and after high temperature

treatment indicates the similar characteristics to those measured in the Slender spindle apple trees on the same rootstock (Fig. 5). On the other hand, inner-crown leaves except of the lowest F_o and V_j , and the highest F_v/F_m showed also the highest V_i (Table 4). However, Φ_{Po} , Ψ_o , Φ_{Eo} and Φ_{Do} in these apple trees were also similar to the Slender spindle apple trees (Fig. 6).

The JIP test parameters obtained from all the combinations of rootstock – crown shape – leaf position after high temperature treatment showed similar Φ_{Po} , Ψ_o , Φ_{Eo} and Φ_{Do} in the 5th and the middle leaves of annual shoots (Fig. 7). However, despite of almost equal Ψ_o and Φ_{Eo} , significantly higher Φ_{Do} in the inner-crown leaves from modified Schlösser palmette apple trees engrafted into rootstock MM.104 led to significantly lower Φ_{Po} than in the Slender spindle apple trees engrafted into rootstock M.9.

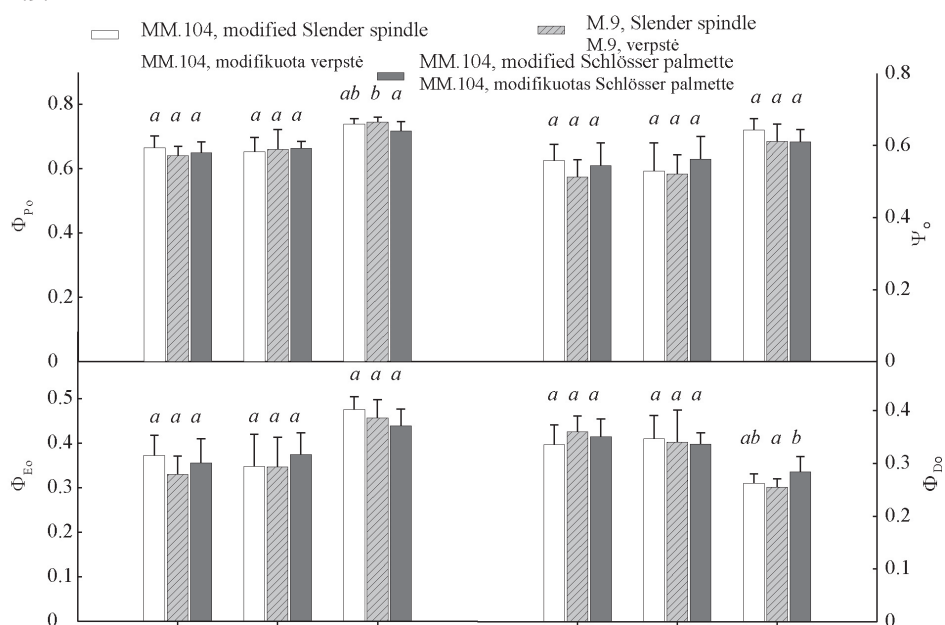


Fig. 7. Comparison of parameters derived from chlorophyll *a* fluorescence induction curves (Φ_{Po} – maximal quantum yield of primary photochemistry, Ψ_o – exciton transfer efficiency to electron transport chain, Φ_{Eo} – electron transport yield, Φ_{Do} – thermal dissipation yield) between treatments (rootstocks and crown shapes) in 5th leaves of east-oriented annual shoots, leaves of middle part of the same shoots and leaves of south-oriented short sprouts on the tree trunks (inner-crown) from apple trees, of cultivar ‘Idared’, after the high temperature treatment (30 min at 42 °C in the dark). Letters indicate statistically significant difference at $P = 0.01$.

7 pav. Išvestinių parametru iš chlorofilo *a* fluorescencijos indukcijos kreivių (Φ_{Po} – maksimali pirminės fotochemijos kvantų išeiga, Ψ_o – eksitono perdavimo į elektronų transporto grandinę efektyvumas, Φ_{Eo} – elektronų transporto išeiga, Φ_{Do} – šilumos sklaidos išeiga), matuotų modifikuotos laibosios verpstės formos ‘Idared’ veislės obelių penktuose lapuose nuo į rytus orientuoto metūglio, lapuose nuo vidurinės šakų dalies ir lapuose nuo į pietus orientuotų vaisinių šakūčių. Analizės atliktos po poveikio aukšta temperatūra (30 min. 42 °C tamspjė). Raidės žymi statistiškai patikimus skirtumus, kai $P = 0,01$.

Discussion. Leaf photosynthetic characteristics are influenced by internal and external factors and reflect their time-space fluctuations. Despite of homogenous rainfall distribution during summer months (Fig. 8), maximal daily air temperatures often exceeded 35 °C, inducing enhanced thermotolerance in apple trees leaves. How was this acclimatory process influenced by type of rootstock, crown shape and leaf topology within the crown?

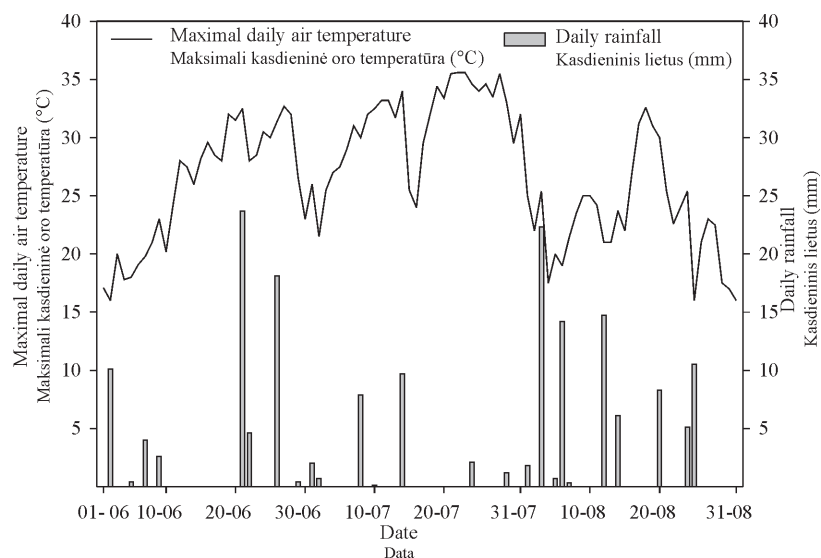


Fig. 8. Course of maximal daily air temperatures and daily rainfall in summer months in 2006, in the experimental orchard of Slovak Agricultural University (Nitra, Slovakia)

8 pav. Maksimalių kasdieninių oro temperatūrų ir kritulių eiga 2006 metų vasaros mėnesiais Slovakijos žemės ūkio universiteto eksperimentiniuose soduose, Nitra, Slovakija

Rootstock mainly influences: (1) the amount and/or ratio of promoting and inhibiting endogenous hormones circulating within tree plant, particularly between the root system and above-ground tree parts; (2) the movement of assimilates (e. g., sugars and amino acids) or mineral elements between the scion and rootstock; and (3) the amount of water taken up and moved through the rootstock to scion (Webster, 1995).

Therefore, we could expect rootstock influence on photosynthetic apparatus as well. Rootstocks with enhanced resistance to *Erwinia amylovora*, provide higher resistance to scion (Jensen et al., 2003). Would it not be possible also in relation to abiotic stressors?

However, no difference in any of the JIP test parameter (Φ_{Po} , Ψ_o , Φ_{Eo} and Φ_{Do}) in leaves with different crown localization, from apple trees engrafted into either vigorous rootstock MM.104 or very dwarfing rootstock M.9 (Fig. 7) implies to the fact that rootstock does not change the PS II thermostability of apple tree leaves. On the contrary, according to Kamboj and Quinlan (1998) and also Kamboj et al. (1999), roots of M.9 accept less auxin and produce less cytokinin and more abscisic acid than MM.104, which is supposed to stress-harden (Wang et al., 2003) the scion in larger extent.

Crown shape optimises light utilization efficiency, but also harmonizes the ratio of fruiting and growing parts of trees. Different branch organisation may also change hormonal composition (auxin-cytokinin ratio) in shoot tips, as mentioned by Tworcoski et al. (2006) and thus also stability of leaf photosynthesis, because cytokinines reduce its susceptibility to heat stress (Liu and Huang, 2002; Gupta et al., 2000). Nevertheless, different crown forms (modified Slender spindle or modified Schlösser palmette) caused no significant change in the PS II thermostability of leaves from any crown position (Fig. 7), suggesting a similar hormonal balance.

Concentrating on PS II reactions to high temperature treatment in leaves from different tree crown positions we detected a pronounced unification in fluorescence induction transients (Fig. 1, 3, 5) and parameters derived from them (Table 4, Fig. 2, 4, 6). The highest electron transport rate to photosystem I (lower disturbances at the acceptor side of PS II reaction centre, different impairment at the donor side are excluded because of balanced F_k/F_j ratio), enhanced communication between antenna complex and reaction centres of the PS II and the reduced thermal dissipation of excitation energy led to the smallest decrease of photochemical PS II efficiency (Strasser, 2004) and thus the highest PS II thermostability in the inner-crown leaves. Response of the 5th and the middle leaves from the annual shoots was very similar.

Reduced chlorophyll *a/b* ratio in the inner-crown leaves from the older apple trees on rootstock MM.104 (Table 2) points to their shaded character (Kull, 2002). Leaves from modified Schlösser palmette apple trees in comparison to modified Slender spindle were likely more exposed to higher light intensities, therefore a slight movement of photosynthetic pigment characteristics was expected to sunny type. However, this was not observed. Because of massive light transmission into the crown of younger apple trees on rootstock M.9, there was no partition into sun and shade type in leaves.

Higher PS II thermotolerance in the inner-crown leaves is in contrast to their shade character, because shade leaves usually contain less xanthophyll cycle pigments (Demmig-Adams and Adams, 1992), less enzymatic and non-enzymatic radical scavengers (Logan et al., 1998) and have reduced photorespiratory activity (Muraoka et al., 2000), thus their protection capacity is reduced.

Also finding of Niinemets et al. (1999) that increased optimal temperature for maximal photosynthetic electron transport in poplar leaves is correlated with integrated quantum flux density, can not be taken into account because of lower PS II thermostability of sun leaves from annual shoots in comparison to shaded inner-crown leaves, no difference between shaded leaves in apple trees with different crown shape, and difference between leaf positions in apple trees engrafted into rootstock M.9. All these results confirm our suggestion that there is no relation between light acclimation syndrome and PS II thermotolerance in the apple tree crowns. So, is the leaf age responsible for the PS II thermostability differences between leaf positions?

Juvenile elm leaves exhibited lower thermotolerance in respect to electron transfer from PS II antenna complex to reaction centre and electron transport to PS I (mainly limited by oxygen evolving complex (OEC) impairment), compared to expanded ones (Jiang et al., 2006). Balanced F_k/F_j in every leaf position in apple trees suggests on reaching comparable OEC stability and hence leaf maturity, and further PS II thermostability rise of the inner-crown leaves provides enhanced communication

between antenna complex and reaction centre of PS II and probably higher capacity of protective mechanisms, utilizing electrons from electron transport chain. Secondly, middle leaves of annual shoots, which are older than 5th leaves, did not exhibit enhanced PS II thermostability. Also different period of elevated temperatures, which are required for photosynthetic apparatus acclimation (Verdaguer et al., 2003), can be excluded, because of limited growth of annual shoots during summer.

Therefore, we suppose that the effect of plant polarity and associated changes in hormonal balance could be responsible for the difference in PS II thermostability in these three leaf positions. Larger proximity to root apices and larger distance from shoot apices shift the hormonal composition in short sprouts on the trunk in favour to cytokinins content, which may reduce leaf susceptibility to heat stress (Liu and Huang, 2002; Gupta et al., 2000). Their effect is probably realized through enhanced antioxidant enzymes level (Liu and Huang, 2002) or photorespiration (Tian et al., 2006).

Conclusions. Fruit trees experiencing extremely high summer temperatures usually exhibit disturbances to photosynthetic process. Testing roles of rootstock vigour (vigorous MM.104 and dwarfing M.9), crown shape and branch organization (Slender spindle and Schlusser palmette) as well as leaf position in apple trees (cv. 'Idared') on photosystem II (PS II) thermostability (parameters derived from rapid chlorophyll *a* fluorescence kinetics) points to no influence of first two factors. On the other hand, the leaf topology seems to be the most important regulatory feature suggesting on influence of trunk/root apex distance associated with cytokinin concentration.

Acknowledgement. This study was supported by the scientific-technical project of the Grant Agency for Applied Research of the Slovak Ministry of Education (AV/1109/2004).

Gauta 2008 04 04

Parengta spausdinti 2008 04 25

References

1. Bukhov N. G., Boucher N., Carpentier R. 1998. Loss of the precise control of photosynthesis and increased yield of non-radioactive dissipation of excitation energy after mild heat treatment of barley leaves. In: *Physiologia Plantarum*, 104: 563–570.
2. Bukhov N. G., Wiese C., Neimanis S., Heber U. 1999. Heat sensitivity of chloroplasts and leaves: Leakage of protons from thylakoids and reversible activation of cyclic electron transport. In: *Photosynthesis Research* 59: 81–93.
3. Cui L. J., Li L. J., Fan Y. M., Xu S., Zhang Z. 2006. High temperature effects on photosynthesis, PS II functionality and antioxidant activity of two *Festuca arundinacea* cultivars with different heat susceptibility. In: *Botanical Studies* 47: 61–69.

4. Demmig-Adams B., Adams W. W. 1992. Photoprotection and other responses of plants to high light stress. In: Annu. Rev. Plant Physiol. Plant Mol. Biol., 43: 599–626.
5. Gupta N. K., Gupta S. Kumar A. 2000. Exogenous cytokinin application increases cell membrane and chlorophyll stability in wheat (*Triticum aestivum* L.). In: Cereal Res. Comm., 28: 287–291.
6. Iba K. 2002. Acclimative response to temperature stress in higher plants: Approaches of gene engineering for temperature tolerance. In: Annu. Rev. Plant Biol., 53: 225–245.
7. Jensen P. J., Rytter J., Detwiler E. A., Travis J. W., McNellis T. W. 2003. Rootstock effects on gene expression patterns in apple tree scions. In: Journal Plant Molecular Biology 53: 493–511.
8. Jiang C. D., Jiang G. M., Wang X., Li L. H., Biswas D. K., Li Y. G. 2006. Enhanced photosystem II thermostability during leaf growth of elm (*Ulmus pumila*) seedlings. In: Photosynthetica 44: 411–418.
9. Kamboj J. S., Blake P. S., Quinlan J. D., Baker D. A. 1999. Identification and quantification by GC-MS of zeatin and zeatin riboside in xylem sap from rootstock and scion of grafted apple trees. In: Plant Growth Reg., 28: 199–205.
10. Kamboj J. S., Quinlan J. D. 1998. The apple tree rootstock and its influence on endogenous hormones. Acta Hort. (ISHS) 463: 143–152.
11. Kull O. 2002. Acclimation of photosynthesis in canopies: models and limitations. Oecologia 133: 267–279.
12. Kuznetsov V. V., Rakitin V. Y., Zholkevich V. N. 1999. Effects of preliminary heat-shock treatment on accumulation of osmolytes and drought resistance in cotton plants during water deficiency. In: Physiologia Plantarum, 107: 399–406.
13. Larcher W. 2003. Physiological plant ecology. Ecophysiology and stress physiology of functional groups. Springer, 513 p.
14. Larkindale J., Huang B. R. 2004. Changes in lipid composition and saturation in leaves in root for heat-stressed and heat-acclimated creeping bentgrass. In: Env. Exp. Bot. 51: 57–67.
15. Law R. D., Crafts-Brandner S. J. 1999. Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase / oxygenase. In: Plant Physiol. 120: 173–181.
16. Lichtenthaler H. K. 1987. Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. Methods in Enzym., 148: 350–382.
17. Liu X. H., Huang B. R. 2002. Cytokinin effects on creeping bentgrass response to heat stress: II. Leaf senescence and antioxidant metabolism. In: Crop Sci., 42: 466–472.
18. Logan B. A., Demmig-Adams B., Adams W. W., Grace S. 1998. Antioxidant and xanthophyll cycle-dependent energy dissipation in *Cucurbita pepo* L. and *Vinca major* L. acclimated to four growth PFDs in the field. In: J. Exp. Bot., 49: 1 869–1 879.

19. Muraoka H., Tang Y. H., Terashima I., Koizumi H., Washitani I. 2000. Contribution of diffusional limitation, photoinhibition and photorespiration to midday depression of photosynthesis in *Arisaema heterophyllum* in natural high light. In: *Plant Cell Env.*, 23: 235–250.
20. Niinemets U., Oja V., Kull O. 1999. Shape of the photosynthetic electron transport versus temperature response curves is not constant along canopy light gradients in temperate deciduous trees. In: *Plant Cell Env.* 22: 1 497–1 513.
21. Pearcy R. W., Muraoka H., Valladares F. 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. In: *New Phytol.*, 166: 791–800.
22. Rahman H. U. 2005. Genetic analysis of stomatal conductance in upland cotton (*Gossipium hirsutum* L.) under contrasting temperature regimes. In: *J. Agr. Sci.*, 143: 161–168.
23. Sairam R. K., Srivastava G. C., Saxena D. C. 2000. Increased antioxidant activity under elevated temperatures: a mechanism of heat stress tolerance in wheat genotypes. In: *Biologia Plantarum* 43: 245–251.
24. Salvucci M. E., Crafts-Brandner S. J. 2004. Inhibition of photosynthesis by heat: The activation state of Rubisco as a limiting factor in photosynthesis. In: *Physiol. Plantarum*, 120: 179–186.
25. Sharkey T. D. 2005. Effect of moderate heat stress on photosynthesis: importance of thylakoid reactions Rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. In: *Plant Cell Env.* 28: 269–277.
26. Schroda M. 2004. The Chlamydomonas genome reveals its secrets: chaperone genes and the potential roles of their gene products in the chloroplast. In: *Photosynthesis Research* 82: 221–240.
27. Srivastava A., Guissă B., Greppin H., Strasser R. J. 1997. Regulation of antenna structure and electron transport in photosystem II of *Pisum sativum* under elevated temperature probed by the fast polyphasic chlorophyll *a* fluorescence transient: OKJIP. In: *Biochim. Biophys. Acta*, 1 320: 95–106.
28. Strasser R. J., Srivastava A., Tsimilli-Michael M. 2000. The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: M. Yunus, U. Pathre, P. Mohanty (eds.): *Probing photosynthesis: mechanisms, regulation and adaptation*. London: Taylor & Francis, 445–483.
29. Strasser R. J., Tsimilli-Michael M., Srivastava A. 2004. Analysis of a chlorophyll *a* fluorescence transient. In: G. C. Papageorgiou, Govindjee (eds.): *Chlorophyll *a* Fluorescence a Signature of Photosynthesis*. Springer, Dordrecht: 321–362.
30. Tian B. J., Wang Y., Zhu Y. R., Lu X. Y., Huang K. Y., Shao N., Beck C. F. 2006. Synthesis of the photo respiratory key enzyme serine: glyoxylate aminotransferase in *C reinhardtii* is modulated by the light regime and cytokinin. In: *Physiologia Plantarum*, 127: 571–582.
31. Tworkoski T., Miller S. S., Scorza R. 2006. Relationship of pruning and growth morphology ratio in shoot of pillar and standard peach trees. In: *J. Plant Growth Reg.*, 25: 145–155.

32. Verdaguer D., Aranda X., Jofre A., El Omari B., Molinas M., Fleck I. 2003. Expression of low molecular weight heat shock proteins and total antioxidant activity in the Mediterranean tree *Quercus ilex* L. in relation to seasonal and diurnal changes in physiological parameters. In: Plant Cell Env. 26: 1 407–1 417.
33. Wang P., Ye J. Y., Shen Y. G., Mi H. L. 2006. The role of chloroplast NAD(P)H dehydrogenase in protection of tobacco plants against heat stress. In: Science in China Series – Life Sciences 49: 311–321.
34. Wang W., Vinocur B., Altman A. 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. In: Planta, 218: 1–14.
35. Webster A. D. 1995. Rootstock and interstock effects on deciduous fruit tree vigour, precocity, and yield productivity. In: New Zealand Journal of Crop and Horticultural Science, 23: 373–382.

SODININKYSTĖ IR DARŽININKYSTĖ. MOKSLO DARBAI. 2008. 27(2).

Vaismedžio vainiko formos, poskiepio ir topologijos įtaka obelių lapų II fotosistemos termostabilumui

P. Ferus, M. Brestič, K. Olšovská, A. Kubová

Santrauka

Vasara obelys dažnai patiria neigiamą aukštų temperatūrų poveikį, kuris gali lemti fotosintezės sutrikimus ir neigiamai paveikti vaisių derlių ir kokybę. Atsižvelgiant į tai, buvo įvertinta poskiepio (žemaūgis M.9 ir augus MM.104), vainiko formos (modifikuota laiboji verpstė ir modifikuota) ir lapų topologijos (lapai imti nuo metinio ūglio virpūnės, vidurio ir nuo vaisinių šakučių) įtaka 'Idared' veislės obelių II fotosistemos (PS II) termostabilumui 2006 metų vasaros pabaigoje. Tirtos chlorofilo *a* fluorescencijos indukcijos kreivės, 30 minučių paveikus tiriamus lapus 42 °C temperatūra. Nei poskiepio tipas nei vaismedžio forma nesukėlė lapo PS II termostabilumo pokyčių, tačiau esminiai skirtumai pastebėti tarp skirtingos lapų pozicijos vaismedžio vainike. Lyginant su lapais nuo metūglio kurie pademonstravo tik nedidelę termotoleranciją, žymus augimas nustatytas lapuose nuo vaisinių šakučių. Išmatuotas PS II termotolerancijos pajėgumas aptartas atsižvelgiant į augalų poliškumo principus.

Reikšminiai žodžiai: II fotosistemos termotolerancija, lapo topologija, obelis (*Malus domestica* Borkh.), poskiepis, vainiko forma.