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Photosynthetic rates and water use efficiencies in three climber species grown in different exposures at urban and suburban sites

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Abstract: Water Use Efficiency and photosynthetic rate of *Fallopia aubertii* (L. Henry) Holub., *Hedera helix* L. and. *Vitis riparia* Michx. grown in various exposures in two site variants: Warsaw city centre vs. suburbs were analysed. All studied climbers showed similar photosynthetic intensity in both sites. The strongest effect of the exposition was found for *F. aubertii*, followed by *V. riparia*, and shade tolerant *H. helix*. WUE of studied climbers was relatively low, higher in suburbs than in the centre, due to lower adaptation to different sites. The WUE of the climbers depended on exposure and the highest scores were obtained for sunny southern and western walls, while the lowest in northern ones. Intrinsic water use efficiency of the studied climbers was higher in the city centre than in the suburbs.

Additional key words: *Vitis, Fallopia, Hedera*, WUE, WUEi, photosynthesis

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Introduction

In urban conditions there is a need to maintain as much plants as possible to provide the inhabitants with at least traces of natural environment. Such plants, however, should meet very high requirements. They must be tolerant to harsh conditions, should form big mass or volume of vegetation of high ornamental value, and along with that they should not occupy too much space. Climbers seem to meet all these conditions. They climb using vertical supports, very often start to grow in deep shadow and finish in full sun. They can also tolerate unfavourable environmental conditions (Carter and Teramura 1988, Bell et al. 1988). Due to the extreme conditions of irradiance and temperature on the walls with different orientation towards sun, growth of climbers on the buildings can be very variable (Borowski et al. 1999). During the day climbers grown in a northern exposure must cope with shade conditions, while those in a southern one with the highest radiation intensity and, possibly, with photoinhibition. Thermal and irradiance conditions present in particular exposures principally affect the basic parameters of gas exchange: photosynthetic intensity and transpiration, stomatal conductance as well as their derivatives – photosynthetic water use efficiencies WUE and WUEi (internal WUE).

In large cities conditions of radiation, temperature and humidity may differ dramatically in the centre and in peripheral localities. To a large extent plant responses to such conditions depend on climbers' characteristics, for instance shade tolerance or radiation demand. It seems that the following three species: *F. aubertii,* reputed as radiation demanding, shade tolerant *H. helix* and *V. riparia,* an intermediate in this respect meet experimental requirements. All these climbers grow both in the city centre and in the peripheries, and may be characterized by quite different manner of climbing.

In this paper an attempt to determine a response of the above mentioned climbers to highly variable growth conditions in a big city agglomeration using changes in basic gas exchange parameters was undertaken.

Methods

During 1997–1999 three species: *F. aubertii* (L. Henry) Holub. (syn.: *Polygonum aubertii* L. Henry, *Bilderdykia aubertii* (L. Henry) Moldenke), *H. helix* L., and *V. riparia* Michx. were studied.

One group of the plants was grown in Warsaw (21°02'E 52°12'N) city center, in urban conditions dramatically changed by a human influence (Chróściel et al. 1990). The remaining group of climbing plants was grown in a suburban area, where the growing conditions are substantially better (Anonymous 1993) (Fig. 1). Climbers were grown on walls with different exposures: from full irradiance on a southern facing walls, throughout intermediate conditions on western and eastern walls, to deeply overshadowed walls in a northern side. They were also subject to different thermal and moisture conditions.

The measurements of gas exchange parameters were done using portable photosynthesis system LI 6200 (Lambda Instrument Corporation, Li-Cor, Lincoln, Nebraska, USA) with leaf chamber of 250 cm^3. CO_2 concentration ranged 400–320 μmol mol^{-1}. There were three plants analysed in dependence on the region and location. For a single measurement we would choose the second, fully developed and healthy leaf from the base of this year long shoot. Each time different leaf was taken for consecutive measurement. The measurements were made on sunny days, light intensity was dependent on the exposure, PPFD ranged from 400 μmol m^{-2} in the northern site to 1800 μmol m^{-2} [PAR] in the southern one. Measurements were performed from 9.00 A.M. to 4.00 P.M. Temperature and humidity were similar during the day, however some small differences among the sites and time of the day were observed. Air flow was kept at the level enabling constant air humidity. Relative air humidity was 60–70%, never overcoming 75%. Parameter K_{abs}, which characterizes water absorption as well as the zero level of CO_2 concentration, was checked just prior to the measurement. On the basis of data obtained the mean photosynthesis (P_N) and water use efficiencies ($WUE=P_N/E$, where E – transpiration rate) (μmol CO_2 mmol H_2O^{-1}) and $WUE_i=P_N/g_s$, where g_s – stomatal conductance (μmol CO_2 mol H_2O^{-1}) were calculated. We measured plants in 48 stands over the period of three years. Each year the measurements were done on one day at the beginning, in the middle and at the end of vegetation season. For each measurement date and each combination nine replicates were made. Results were compared using ANOVA (Statgraphics I.T.).

Results

Photosynthesis of climbers grown in different exposures

The least mean photosynthetic rate from among analysed climbers, measured for all exposures in both regions was recored for *V. riparia* (3.40 μmol CO_2 m^{-2} s^{-1}), although it did not differ significantly from that

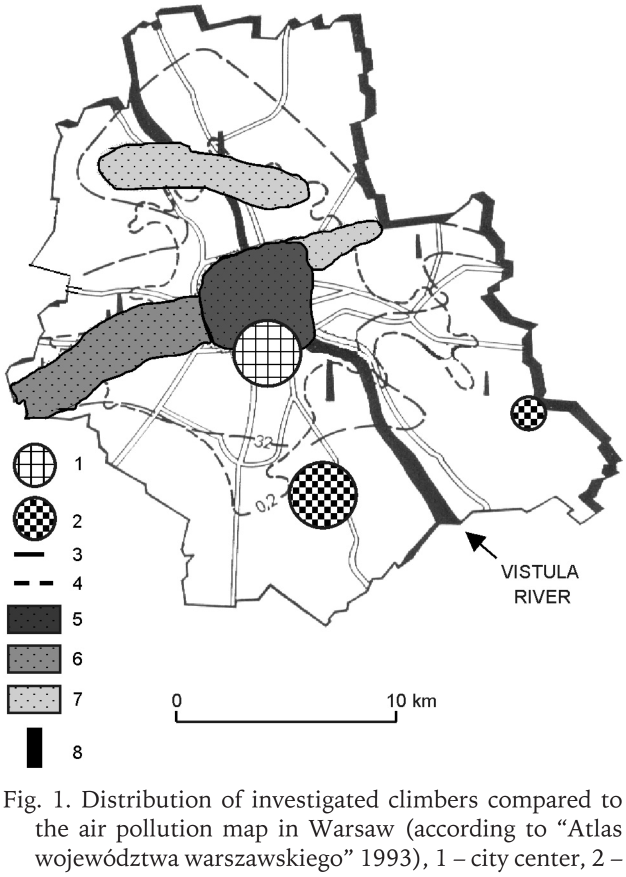

Fig. 1. Distribution of investigated climbers compared to the air pollution map in Warsaw (according to "Atlas województwa warszawskiego" 1993), 1 – city center, 2 – suburbs, 3 – calculated range of average annual SO_2 concentration from combustion processes (norm 32 μg m^{-3} a^{-1}), 4 – calculated range of average annual Pb from traffic (norm 0,2 μg m^{-3} a^{-1}), 5 – region of excessive air pollution, 6 – region of enhanced air pollution, 7 – region of increased air pollution, without surpassing accessible norm, 8 – the highest level of atmospheric pollution

Table 1. Analysis of Variance for photosynthetic rate (P_N)

Source	Sum of Squares	Df	Mean Squere	F – Ratio	P – Value
MAIN EFFECTS					
A: SPECIES	1 574.29	2	787.147	90.07	0.0000
B: REGION	128.981	1	128.981	14.76	0.0001
C: EXSPOSURE	4 581.72	3	1 527.24	174.70	0.0000
INTERACTIONS					
AB	148.73	2	74.36	8.51	0.0002
AC	1 721.88	6	286.979	32.84	0.0000
BC	198.678	3	66.226	7.58	0.0000
ABC	453.68	6	75.6133	8.65	0.0000
RESIDUAL	16 386.7	1875	8.73959		
TOTAL (CORRECTED)	25 197.5	1898			

of *H. helix* (3.72 μmol CO_2 m^{-2} s^{-1}). The highest photosynthetic rate was found for *F. aubertii* (5.48 μmol CO_2 m^{-2} s^{-1}). It differed significantly from the remaining species (Table 1).

Exposure clearly affected photosynthetic rate of the studied climbers. It increased in plants growing on south facing walls, the effect was weaker in western ones, and the weakest in northern walls. Generally, photosynthetic rate of climbers growing in northern and eastern exposures (2.68 and 3.03 μmol CO_2 m^{-2} s^{-1}, respectively) was nearly the same, as compared to western (4.41 μmol CO_2 m^{-2} s^{-1}) and southern (6.64 μmol CO_2 m^{-2} s^{-1}), the latter significantly differed from the others (Table 1).

Significant differences in photosynthetic rate for interaction species vs exposures were found (Table 1). *Hedera. helix* photosynthesized on northern one (3.31 μmol CO_2 m^{-2} s^{-1}) better than other species. Photosynthetic rate was higher when compared to the other climbers in the same exposure (Fig. 2). Average photosynthetic rate of *H. helix* in southern exposure (4.69 μmol CO_2 m^{-2} s^{-1}) was lower than for the other species. Differences in photosynthesis among southern exposure and the others for *Hedera helix* were smaller than in the case of *F. aubertii* and *V. riparia* (Fig. 2).

Mean photosynthesis of *F. aubertii* was more than three times higher in south facing walls when compared to northern exposures. This species also photosynthesized well on western exposures when compared to eastern, and especially to northern ones. Photosynthesis of *F. aubertii* in southern (9.76 μmol CO_2 m^{-2} s^{-1}) and western (6.14 μmol CO_2 m^{-2} s^{-1}) exposures was higher than that in the same exposures for *H. helix* (4.69 and 3.44 μmol CO_2 m^{-2} s^{-1}, respectively) and *V. riparia* (5.47 and 3.64 μmol CO_2 m^{-2} s^{-1}, respectively) (Fig. 2).

For *V. riparia* photosynthetic rate was the highest in southern exposures follwed by that in western facing walls, then eastern ones, and the lowest in northern exposures. The photosynthetic rate between exposures for *V. riparia* exhibited smaller variation than

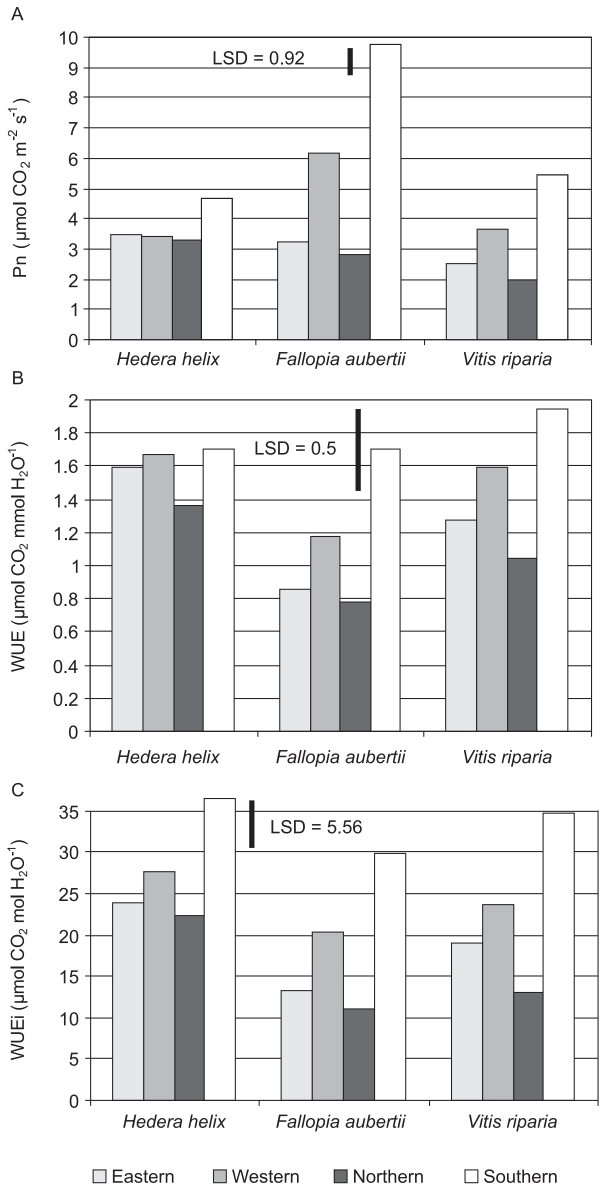

Fig. 2. Average photosynthetic rate (P_N) – A, water use efficiency (WUE) – B, intrinsic water use efficiency (WUE_i) – C, of climbers grown in four exposures

for *F. aubertii*, but higher than in the case of *H. helix* (Fig. 2).

Photosynthesis of climbers grown in different regions (center-suburbs)

It was found that photosynthesis of climbers in the city centre (3.94 μmol CO_2 m^{-2} s^{-1}) was significantly lower than in the suburbs (4.46 μmol CO_2 m^{-2} s^{-1}) (Table 1). The largest difference between city centre (2.80 μmol CO_2 m^{-2} s^{-1}) and suburbs (3.99 μmol CO_2 m^{-2} s^{-1}) was noted for *V. riparia*. Slightly higher photosynthesis in suburbs than in the city centre was recorded for *F. aubertii,* while the opposite was found for *H. helix*: this species showed slightly higher photosynthetic rate in the city centre than in the suburbs (Fig. 3).

WUE of climbers grown in different exposures

The differences in plant responses to environmental factors can be seen in photosynthetic water use efficiency – WUE. Its highest value was found for *H. helix* (1.57 μmol CO_2 mmol H_2O^{-1}), lower (1.46 μmol CO_2 mmol H_2O^{-1}) was recorded for *V. riparia*. *Fallopia aubertii* showed the lowest WUE – 1.13 μmol CO_2 mmol H_2O^{-1}, all values differed significantly (Table 2).

WUE was highly affected by exposure. The lowest was noted for northern exposures (1.06 μmol CO_2 mmol H_2O^{-1}), while the highest for southern ones (1.78 μmol CO_2 mmol H_2O^{-1}). In the case of *H. helix* WUE is nearly constant for all exposures, the largest differences being between northern (1.36 μmol CO_2 mmol H_2O^{-1}) and southern (1.70 μmol CO_2 mmol H_2O^{-1}) ones. The highest differences among the exposures were found for *F. aubertii*, especially between northern (0.78 μmol CO_2 mmol H_2O^{-1}) and southern (1.70 μmol CO_2 mmol H_2O^{-1}) facing walls. For *V. riparia* differences between northern and southern ex-

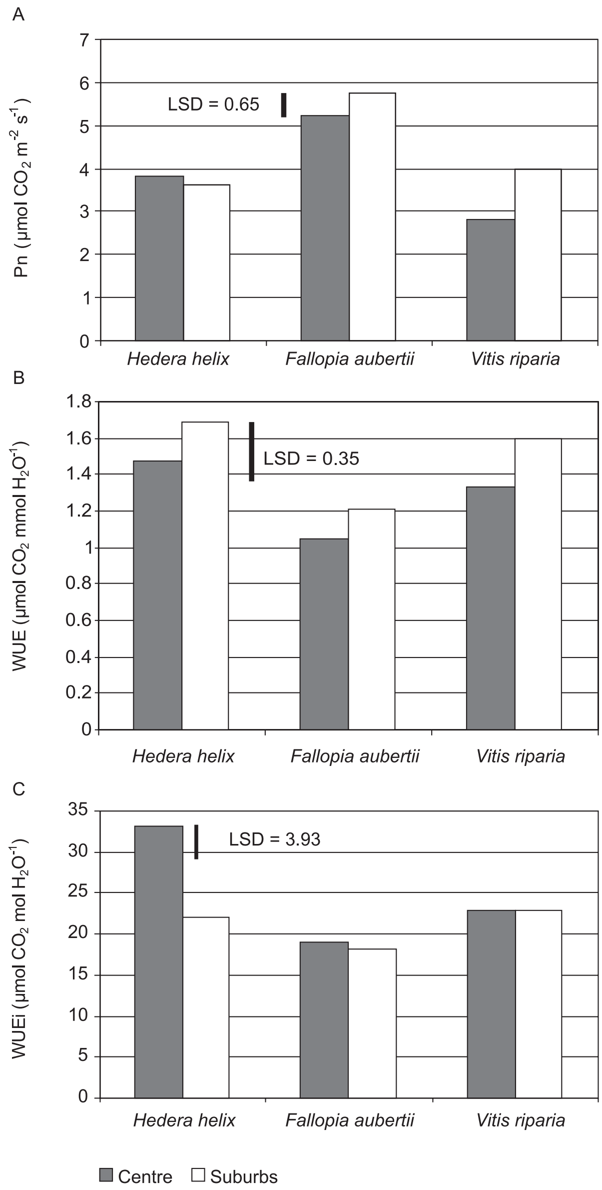

Fig. 3. Average photosynthetic rate (P_N) – A, water use efficiency (WUE) – B, intrinsic water use efficiency (WUE_i) – C, of climbers grown in the city center and suburbs

Table 2. Analysis of Variance for WUE

Source	Sum of Squares	Df	Mean Squere	F – Ratio	P – Value
MAIN EFFECTS					
A: SPECIES	68.0742	2	34.0371	54.45	0.0000
B: REGION	22.0463	1	22.0463	35.27	0.0000
C: EXSPOSURE	140.246	3	46.7487	74.78	0.0000
INTERACTIONS					
AB	1.02259	2	0.511295	0.82	0.4415
AC	28.8467	6	4.80779	7.69	0.0000
BC	17.3333	3	5.77775	9.24	0.0000
ABC	13.4188	6	2.23647	3.58	0.0016
RESIDUAL	1172.1	1875	0.625117		
TOTAL (CORRECTED)	1459.27	1898			

Table 3. Analysis of Variance for WUE_i

Source	Sum of Squares	Df	Mean Squere	F – Ratio	P – Value
MAIN EFFECTS					
A: SPECIES	25741.9	2	12871.0	40.53	0.0000
B: REGION	7746.2	1	7746.0	24.39	0.0000
C: EXSPOSURE	87770.0	3	29256.7	92.14	0.0000
INTERACTIONS	12069.1	2	6034.56	19.00	0.0000
AB	2285.62	6	380.937	1.20	0.3035
AC	10809.2	3	3603.07	11.35	0.0000
BC	10898.6	6	1816.43	5.72	0.0000
ABC	595374.0	1875	317.533		
RESIDUAL					
TOTAL (CORRECTED)	751846.0	1898			

posures were similarly large, the last value was the highest score obtained for all studied climbers (Fig. 2).

WUE of climbers grown in different regions (city center-suburbs)

Water Use Efficiency for all studied climbers was significantly smaller in the city center (1.28 μmol CO_2 mmol H_2O^{-1}) than in the suburbs (1.50 μmol CO_2 mmol H_2O^{-1}) (Table 2, Fig. 3).

WUE_i of climbers grown in different exposures

From all studied climbers the lowest WUE_i was found for *F. aubertii* (18.60 μmol CO_2 mol H_2O^{-1}), intermediate for *V. riparia* (22.88 μmol CO_2 mol H_2O^{-1}) and the highest for *H. helix* (27.61 μmol CO_2 mol H_2O^{-1}). It was the lowest in northern exposures (15.05 μmol CO_2 mol H_2O^{-1}), reaching 18.31 μmol CO_2 mol H_2O^{-1} in eastern, and 23.51 μmol CO_2 mol H_2O^{-1} in western exposures. The highest WUE_i, 33.58 μmol CO_2 mol H_2O^{-1}, was noted for southern exposures, all values differed significantly (Table 3).

Individual plants showed exceptionally high variation of WUE_i depending on exposure. The highest WUE_i for *H. helix* was recored in southern exposure (36.55 μmol CO_2 mol H_2O^{-1}), the result being the highest value for all studied climbers in all exposures. On the other hand values of WUE_i for *H. helix* were less variable across exposures. For *V. riparia* there was more than twofold difference between northern (14.00 μmol CO_2 mol H_2O^{-1}) and southern (34.75 μmol CO_2 mol H_2O^{-1}) exposures. In the case of *F. aubertii*, the values of WUE_i were the lowest for all exposures as compared to corresponding exposures for the remaining climber species, yet again the resulting values for southern exposure (29.73 μmol CO_2 mol H_2O^{-1}) were three times higher when compared to north facing walls (11.12 μmol CO_2 mol H_2O^{-1}) (Fig. 2).

WUE_i of climbers grown in different regions (city center – suburbs)

In all cases WUE_i was higher in the city center (25.05 μmol CO_2 mol H_2O^{-1}) than in the suburbs (21.01 μmol CO_2 mol H_2O^{-1}), values differed significantly (Table 3). The biggest differences were noted for *H. helix*: WUE_i in the city center was 33.18 μmol CO_2 mol H_2O^{-1}, while in the suburbs 22.04 μmol CO_2 mol H_2O^{-1}. For the remaining two climber species the values were significantly lower. Among them *V. riparia* performed nearly at the same level in the city center and in the suburbs (Fig. 3).

Discussion

Harsh growing conditions in the city centre caused decrease in photosynthetic rate of *V. riparia* leaves and, to much less extent, *F. aubertii*. Tendency for higher intensity of photosynthesis in the centre of the town found for *H. helix* can indicate higher tolerance of ivy to environmental limitations in the city centre.

The biggest differences in photosynthetic rate found between southern and western exposures and the remaining ones for *F. aubertii* indicate higher radiation demand of this species. Large differences in photosynthetic intensity between similarly illuminated western and eastern exposures probably resulted from basic differences in temperature in very warm western exposition and cooler eastern one (Borowski, data not shown). Furthermore higher humidity in shaded exposures may serve as an explanation.

The smallest differences in photosynthetic rate in the studied exposures were observed for *V. riparia*. This result may indicate slightly smaller radiation needs of this species as compared to *F. aubertii. Vitis riparia in this respect* slightly differs from *V. vinifera,* which grows most effectively in well irradiated places (Carter et al. 1989). *Vitis riparia* showed the lowest photosynthetic rate in northern exposures (with clearly the worst radiation conditions) and therefore one should expect that according to Borowski et al. (1999) such a low photosynthetic rate will limit growth in shaded places.

Hedera helix, reputed as a shade-tolerant (Heieck 1992), showed a slight increase in photosynthetic intensity in southern exposures as compared to other studied species. We found differences in photosynthetic rate of *H. helix* among studied exposures but Yang et al. (2006), who studied *H. nepalensis* var. *sinensis,* found differences for different types of leaves (from creeping, climbing and reproductive branches). In our study only leaves from climbing branches were considered.

Relatively high intensity of photosynthesis recorded in cooler northern and eastern exposures might result from better adaptation of this native ivy to temperate cold climate as compared to other species originating from warmer climatic region (*Fallopia* from China, mainly from Tibet and *Vitis* from Central and Eastern North America).

Photosynthetic rate of analysed climber species correspond to data for *Parthenocissus quinquefolia* grown in the city centre and in the suburbs of Warsaw (Borowski, 1996), however our values for photosynthesis were on average lower (3.94–4.46 vs. 8.19–8.81 μmol CO_2 m^{-2} s^{-1}, respectively).

Differences in mean photosynthesis among studied species were, to a large extent, caused by differences in photosynthesis in individual exposure. High average photosynthetic rate of *F. aubertii* was mainly a result of high photosynthetic intensity of plants displayed in both well irradiated exposures (southern and western).

Relatively low P_N values in our experiment as compared to those found in literature (Carter and Teramura 1988, 1989, Castellanos 2009, Teramura et al. 2009) resulted from presenting average photosynthetic rates instead of maximal photosynthetic rates obtained from light curves. For instance, in our experiments *H. helix* showed mean P_N at a level of 6 μmol CO_2 m^{-2} s^{-1} in southern exposures and about 8 μmol CO_2 m^{-2} s^{-1} in western ones, while e.g. Castellanos (2009) presented maximal P_N of about 14 μmol CO_2 m^{-2} s^{-1}.

Also WUE values differed among species and combinations. The highest average values of photosynthetic water use efficiency for *H. helix* might result from its winter endurance, and especially from anatomic structure of the leaves (Heieck 1992). The lowest WUE values were found for *F. auberti,* a plant with small, thin and naked leaves. Intermediate values of WUE recorded for *V. riparia* might be associated with the presence of dense, numerous hairs on the leaf surface.

Higher WUE in the suburbs than in the city center resulted from higher photosynthesis rather than transpiration, which was nearly the same for all studied species. Due to smaller soil contamination and air pollution in suburban conditions when compared to those in the city centre much better air transparency and more radiation is available there.

Both, the highest WUE values and photosynthetic rate were observed in the southern exposure, and the lowest in the north facing walls. It reflects similar changes of transpiration rate. In the case of *F. aubertii* its relatively low WUE and high photosynthetic rate as compared to other species indicates much higher transpiration than in other climbers. Average values of WUE for the studied species are much lower than those obtained by Yoshie (1986) for many plant species, mainly for annuals.

Different levels of radiation and temperature observed in all four exposures did not affect significantly the relationship between transpiration and stomatal conductance. This can be proved by similar patterns of WUE and WUE_i (Fig. 4–6). On the other hand, worse habitat conditions prevailing in the city centre greatly influenced WUE value, which, in turn, changed the trend observed for WUE_i. This indicates the great influence such conditions have on photosynthetic water economy, i.e. lower stomatal conductance in the city centre than in suburbs.

The highest stomatal conductance among climbers, nearly twice bigger than for other studied species was recorded for *F. aubertii* grown in southern exposure (0.27–0.33 *vs* 0.14–0.16 mol H_2O m^{-2} s^{-1}). It is confirmed by Givnish (1988) in the case of sunny plants. The same pattern of WUE and WUE_i changes shows that there is no influence of the environment on transpiration rate. Clearly changed pattern of these indices in the centre and in the suburbs revealed such influence, at the same photosynthetic rate quite different changes of transpiration and stomatal conductance of climbers leaves were observed (Łoboda et al. 1998).

Our data concerning gas exchange allow to classify *V. riparia* as an intermediate species between sun-demanding *F. aubertii* and shade tolerant *H. helix*. Having stomatal conductance at the same level as *H. helix, Vitis* shows the reaction to improvement of radiation conditions which resembles that of *Fallopia.*

The analyzed climbers show specific for the whole group physiological plasticity that enables them to grow under variable environment conditions (Carter et al. 1989). *Hedera helix,* among analyzed climbers, seems to be the best adapted for growing under urban conditions. It forms a big mass of evergreen leaves, more densely covers walls and reaches an impressive height. Although not growing too fast, due to its physiological plasticity it equally well grows in each exposure, including the south facing walls (when the soil is moist enough). The latter finding is against common opinions (Baumann 1991, Heieck 1992). *Vitis riparia* prefers southern exposures, nevertheless it can grow in other sites. Our studies confirmed common opinions on *F. aubertii*. This fast-growing climber should be planted only in well illuminated southern and western exposures, never against north facing walls. This finding supports the data of Borowski et al. (1999), who analyzed the growth (shoot increments, leaf area index LAI) of the same species.

In our experiments exposure of climbers decided of their sunny or shade character. It means that the physiological and morphological adaptations of studied species to changing light environment (Castellanos 2009, Teramura et al. 2009) were limited.

Conclusions

1. Water use efficiency of studied climbers is relatively low: higher in suburbs than in the city centre, this finding suggests their low adaptation to different habitats.
2. The WUE of the climbers depends on exposure. It is higher in sunny exposures (southern and western) and lower in shaded sites, and indicates clear dependence of WUE on photosynthetic rate.
3. Intrinsic water use efficiency (WUE_i) of the studied climbers is higher in the city center than in the suburbs, due to the lower stomatal conductance in the city center, accompanied by similar photosynthetic rate in both sites.
4. The values of WUE_i and photosynthetic rates in different exposures showed almost the same pattern, what can suggest the dominance of photosynthetic rate over stomatal conductance in this index.
5. Analysed climbers grown in Warsaw city center and in suburbs display similar photosynthetic intensity in both regions.
6. Photosynthetic intensity of climbers depends on the exposure. The most responsive was sun-demanding *F. aubertii*, *V. riparia* being intermediate in this respect showed lower photosynthetic intensity, followed by shade tolerant *H. helix*.
7. *Hedera helix* shows the lowest level of variation in photosynthetic rate both between sites and exposures.

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