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The Effect of Photosynthesis Parameters on Leaf Lifespan

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Abstract—Leaf longevity (LL) varies widely among higher plants. LL is a sum of the functional component LL_f (the duration of active photosynthesis) and the nonfunctional component LL_n (duration of the period during which photosynthesis does not occur). LL_n corresponds to the period of winter dormancy in the case of evergreen boreal species. The photosynthetic potential of the leaf (PPL)—that is, the maximal possible amount of CO_2 fixed during the leaf lifespan—is inferred from the dynamics of the maximal rate of photosynthesis (P_a) during LL_f. P_a reaches a peak value ($P_{a\,\max}$) during leaf “maturation.” The photosynthetic potential depends on the functional lifespan to a greater degree than on the maximal rate of photosynthesis. The PPL/LL_f ratio determines the rate of realization of the photosynthetic potential during the lifetime of the leaf. LL_f is strongly and positively correlated to LL, and LL can therefore be considered a parameter determining the rate of PPL realization, along with LL_f (for a first approximation). The prolonged LL_f characteristic of evergreen species gives them an advantage—a higher photosynthetic potential than that of deciduous species. Consequently, PPL is realized more slowly in evergreen species than in deciduous species. An increase of LL_f and LL is accompanied by an increase of leaf construction cost (LCC_a) and a decrease of the photosynthesis rate, with the decrease per unit dry weight (P_m) being much more pronounced than that per unit leaf area (P_a). This points to a much higher contribution of cell wall weight to the total dry weight of long-lived leaves of evergreen species than to that of short-lived leaves of deciduous species. Unidirectional changes of PPL and LCC_a stabilize leaf payback (LP). Species with a short (long) LL_f and high (low) rate of PPL realization are characteristic of early (late) succession and habitats with favorable (unfavorable) environmental conditions for photosynthesis and growth, since these species are more competitive under said conditions. Species with a high rate of PPL realization have an advantage in competition under conditions favorable for photosynthesis and growth, since they use environmental resources for rapid growth and expansion. The rate of photosynthetic potential realization characterizes the aging rate of the leaf.

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INTRODUCTION

The leaf can be considered the fundamental unit of energy in biology, since it mediates the flows of energy and matter in all terrestrial ecosystems (Blonder et al., 2011). The time during which the leaf fulfills its photosynthetic function is of great importance for the life of the plant and the whole ecosystem. This time can be defined as the lifespan of the leaf (LL, leaf longevity) for a first approximation. The time of leaf development inside the bud varies greatly between species, and LL is therefore usually defined as the interval between the emergence of the leaf from the bud and its abscissin (Kikuzawa, 1995). Leaf longevity is considered one of the main parameters of carbon economy in plants (Wright et al., 2002). Some researchers regard this value as one of the morphological characteristics of plants (Haddad et al., 2004), but it is actually in a closer relationship to the functional characteristics of a plant due to its indirect connection to photosynthesis and transport of photosynthates (Wright et al., 2004).

LL in higher plants may vary considerably, ranging from several weeks to more than 40 years in different species (Richardson et al., 2010). LL may vary by two to four times within a single species and even within an individual plant (Warren and Adams, 2001; Lizaso et al., 2003; Tucic et al., 2003; Haddad et al., 2004; Vasfilov, 2005); therefore, the similarity of LL in different, sometimes taxonomically distant, species is surprising (Reich, 1999; Lusk et al., 2003). The causes of such variability are of great interest.

LL is usually analyzed in the middle generation of leaves of various forms of higher plants, such as trees, vines, bushes, shrubs, or herbs. LL variability is much more pronounced in trees than in herbs, and trees are often chosen as objects of research. However, despite the abundance of factual material, a comprehensive theory explaining LL variability does not yet exist (Lusk and Corcuera, 2011). The author of the present article believes that variation in leaf longevity is associated with the main function of the leaf, i.e., photosynthesis, and therefore it is necessary to tackle the problem of estimating the amount of CO_2 assimilated by the leaf during its lifespan. Attempts at such an evaluation (Kikuzawa, 1991; Falster et al., 2012) are not devoid of drawbacks, in the author’s opinion, and therefore the information content of the values obtained is low. First, the approach used for calculation is not completely validated. Second, the parameters used are redundant to a certain extent, and the inconsistency of the dimensions results in the emergence of dimensionless values, such as g C g^{-1} C (Kikuzawa and Lechowicz, 2006; Falster et al., 2012).

Estimates of the leaf economical spectrum, which serves as a measure of environmental variability between plant species, based on the cost of photosynthesis products required for growth, development, and subsequent functioning of the leaf (Westoby et al., 2013) are not free of drawbacks, in the author's opinion. The authors of this approach emphasize the spectrum of leaf economy, rather than that of photosynthetic metabolism, as the subject of the analysis; in other words, photosynthesis is reportedly viewed as a system of carbon dioxide assimilation in its entirety rather than a set of individual reactions. This is formally true; however, the assessment of the spectrum of leaf economy is based on interpretation of photosynthesis rate measurements performed with saturating irradiance per unit of leaf area (P_a) and per unit dry weight (P_m), and the biological meaning of these parameters should therefore be approached with caution, as was emphasized in a recent discussion (Lloyd et al., 2013). The leaf-economy spectrum also characterizes the construction costs of the duration of leaf and photosynthesis, which provides for the recovery of carbon compounds consumed during leaf formation and functioning (Reich et al., 1997; Wright et al., 2004; Westoby et al., 2013). Leaf construction costs, like the photosynthesis rate, can be normalized either to dry weight (LCC$_m$, leaf construction cost per dry mass) or to leaf area (LCC$_a$). Leaf payback time (LP$_t$) is assessed with the use of LCC$_m$ and P_m values (Poorter et al., 2006; Coste et al., 2011). LP$_t$ is expressed in the number of light days of photosynthesis required for the fixation of an amount of CO$_2$ equivalent to the dry weight of a mature leaf. LP$_t$ analysis in a range of species showed that the values of this parameter always exceeded the LL value (Coste et al., 2011). Since LCC$_m$ varies very slightly between species (Kikuzawa and Lechowicz, 2006), LP$_t$ is highly dependent on the rate of photosynthesis estimated as P_m (i.e. per unit dry weight), which can deviate significantly from the P_a photosynthesis rate (per unit leaf area) (Lloyd et al., 2013). Therefore, the LP$_t$ parameter is of little use in comparing different species.

The present study summarizes the published material to propose approaches to the assessment of photosynthetic potential, the rate of its realization, leaf construction cost, and leaf payback. The possible reasons for the considerable variation in leaf longevity in higher plants are addressed via analysis of the determined parameters.

FUNCTIONAL LIFESPAN OF THE LEAF

Photosynthetic activity is usually assessed as the CO$_2$ absorption rate per unit leaf area (P_a), fresh or dry weight (P_m), chlorophyll content, or protein content (Voznesenskii et al., 1965). The photosynthesis rate depends on many factors, especially on illumination, and therefore the photosynthesis measurements included in comparative studies are performed with saturating illumination of the leaf when the curve characterizing P_a dependence on illumination reaches a plateau of maximal values. The potential rate of photosynthesis, rather than photosynthesis rate in situ, is actually measured. Ecology studies involve P_a measurements in "mature" leaves, for which growth and development, including the development of the photosynthesis system (chloroplast population of the leaf), are complete. The P_m parameter is widely used in ecology studies, since it is correlated to a range of functional characteristics of the leaf, in contrast to P_a (Lloyd et al., 2013). These two parameters can be interconverted (Cernusak et al., 2008) with the equation

$$P_m = P_a : \text{LMA}, \tag{1}$$

where LMA is leaf dry mass per unit area. As a rule, P_a and LMA are measured, and P_m is determined with equation (1).

The functional longevity of the leaf (LL$_f$) represents the total number of days when $P_a > 0$. If the total number of days when photosynthesis does not occur in the leaf ($P_a = 0$) is denoted as LL$_n$, LL can be represented as a sum:

$$\text{LL} = \text{LL}_f + \text{LL}_n. \tag{2}$$

LL$_f$ = LL if LL$_n$ = 0. This is observed, for example, in tropical rainforest species exposed to the major environmental factors favoring photosynthesis throughout the year. LL$_n$ corresponds to the period of winter dormancy when $P_a = 0$ in boreal evergreen species, and LL$_f$ corresponds to the difference between LL and LL$_n$ in this case. The case of plants growing in areas characterized by drought periods and constantly positive temperatures is more complicated. LL$_f$ = LL for deciduous species that shed their leaves during the dry season, while the days of the dry period when $P_a = 0$ during all the daylight hours are included in LL$_n$ for evergreen species. The quantification of this number of days in field studies obviously is very time-consuming and technically challenging. This problem occurs if LL$_f$ estimation in species growing in arid regions is attempted. The estimation can be performed if it is assumed that photosynthesis in evergreen species is limited to early morning and/or evening hours during the dry period and the photosynthesis rate is low. Thus, the dry period days with low P_a can be attributed to LL$_f$.

The relationship between the average temperature and the number of days favorable for photosynthesis proposed in (Kikuzawa, 1996) (Fig. 1) can be used to assess the LL$_f$ during the year. This relationship is

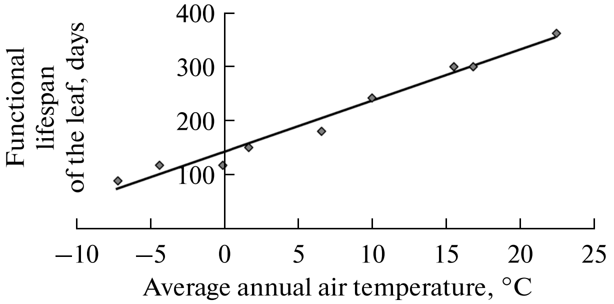

Fig. 1. Dependence of the number of days favorable for photosynthesis per calendar year on the average annual temperature of the plant habitat. The regression equation: $y = 9.5x + 146$, $r = 0.99$, $p < 0.001$, $r^2 = 0.98$. According to (Kikuzawa, 1996) with the author's modifications.

based on a positive correlation between temperature, on one hand, and the rates of photosynthesis, growth, and transport of photosynthates (Lyubimenko, 1963; Leopold, 1960; Kursanov, 1976; Muller et al., 2011; Pantin et al., 2012). LL_f calculated according to this procedure can be termed calendar or annual functional longevity of the leaf. The regression equation (Fig. 1) shows that LL_f can amount to 365 days per year at an average annual temperature of 23°C and above, provided that seasonal droughts blocking photosynthesis do not occur. It should be noted that the relationship between the average annual temperature and the number of days favorable for photosynthesis is not relevant for deciduous species, since LL is lower than 365 days per year and equal to LL_f in these species. The ontogenesis of leaves of deciduous species of the boreal zone is completed prior to the beginning of the unfavorable period, such as winter dormancy. A range of tropical rainforest species are characterized by LL values lower than a year and can be considered deciduous. These plants shed all leaves simultaneously and start producing new leaves after a short time (Richards, 1952). One to three generations of leaves are produced by such species within a year.

The LL for evergreen species exceeds one year, and the LL_f for these species is determined by multiplying the ratio of LL (in days) to 365 (days) by the LL_f (Fig. 1). Tropical rainforest species produce new leaves and shed the old ones continuously, and therefore the tree crown is always green (Richards, 1952). A decrease in illumination is the main factor contributing to increased lifespan of leaves in the tropical zone, where $LL = LL_f$ (Coste et al., 2011; Lusk and Corcuera, 2011). The advancement of plants into cold northern latitudes or highlands of the boreal zone is accompanied by increased LL (Pravdin, 1964; Starostin, 1974; Walter, 1973; Ewers and Schmid, 1981; Ewers, 1982; Kikuzawa, 1991). The advancement of evergreen species in the direction of decreasing annual temperature of the habitat is accompanied by increased LL (Zhang et al., 2010). A decrease in temperature is associated with reduced rates of plant growth and photosynthesis, and therefore the temperature is the main factor of LL increase in the boreal zone and the highlands (Leopol'd, 1968; Pantin et al., 2012). However, the air temperature is associated with the intensity of solar radiation, and a temperature decrease is usually accompanied by a decrease in illumination. LL_n increases and LL_f decreases concomitantly to the decrease of the average annual temperature in such zones, and therefore the LL value for the same evergreen species can vary by several years (Pravdin, 1964; Ewers and Schmid, 1981). Notwithstanding the increase in LL_n and a respective decrease in LL_f per calendar year (at a LL of 365 days) upon the advancement of evergreen species towards the north, the total LL_f of a leaf does not decrease but rather increases due to the prolongation of LL by several years. Data on the combined effect of light and temperature within the crowns of pines are indicative of an increase in LL_f; the LL of the needles is lower and the P_a is higher in the upper part of the crown, which is illuminated and heated more efficiently than the lower part, regardless of the genotypic homogeneity of the needles (Sudachkova et al., 1990; Warren and Adams, 2001; Vasfilov 2005; Niinemets et al., 2007). The LL_n is similar for all needles within a tree crown, and therefore the increase of LL in the lower part of the crown characterized by less favorable photosynthesis conditions is enabled by a change in LL_f.

Thus, the following pattern is traced for the leaves of several higher plant species, mainly evergreen conifers: the deterioration of environmental conditions for photosynthesis is accompanied by an increase in the duration of leaf functioning. This variation pattern accounts for the stabilization of the total amount of CO_2 assimilated by the leaf during the photosynthesis period.

PHOTOSYNTHETIC POTENTIAL AND THE RATE OF REALIZATION THERE OF DURING LEAF ONTOGENESIS

Species with a long leaf lifespan are widely assumed to assimilate larger amounts of carbon dioxide over their lifetimes, since they have more time available for CO_2 fixation (Falster et al., 2012). However, an LL increase is accompanied by a P_a decrease, as was mentioned above. This implies the stability of the CO_2 amount is fixed over the lifetime of the leaf rather than an increase of this value, at least within a single species. The amount of CO_2 fixed over the whole lifetime of the leaf must be determined in order to characterize the actual relationship between LL and the amount of CO_2 assimilated. Continuous measurements of CO_2 absorption by a leaf throughout its lifetime present a technically complex and extremely time-consuming task that obviously cannot be incorporated into large-scale ecology studies; therefore, it is necessary to develop an approach to derive the amount of CO_2 assimilated during the lifetime of the leaf from a small number of photosynthesis rate measurements. The maximal photosynthesis rate P_a characterized by such measurements is determined for a completely mature leaf exposed to saturating illumination. The amount of carbon assimilated by a leaf during its lifetime is estimated with the P_a value (Kikuzawa and Lechowicz, 2006; Falster et al., 2012). However, the amount of carbon calculated according to this approach is a dimensionless quantity ($\mathrm{g}\,C\,\mathrm{g}^{-1}\,C$).

The method for calculating the amount of CO_2 fixed over the lifetime of the leaf proposed in the present study requires the maximum rate of photosynthesis P_a and functional leaf longevity LL_f as the input data. This parameter characterizes the potential, i.e. the maximal possible, amount of CO_2 fixed by the leaf over its lifetime, and can be defined as the photosynthetic potential of the leaf (PPL). The PPL calculation is based on P_a dynamics over the LL_f.

P_a changes during leaf ontogenesis can be described by a unimodal curve with a maximum usually observed at a time point preceding the termination of leaf growth (Mokronosov, 1981, p. 96). A pattern of P_a change involving an increase to a maximum during the "maturation" period and a subsequent decrease has been reported by other researchers as well (Hikosaka, 2005; Warren, 2006; Pantin et al., 2012). P_a is close to zero by the end of the lifetime of the leaf, and the pattern of change of maximal P_a assessed at saturating illumination of the leaf is similar to that of P_a (Kuo et al., 2009). These data make it possible to define P_a dynamics throughout the leaf ontogenesis by the function $y = dP_a/dt$, which has two minima ($P_a = 0$) at $t = 0$ and $t = LL_f$ and one peak ($P_a = P_{a\,\max}$) during the "maturation" of the leaf. A P_a decrease is one of the signs of leaf aging (Wingler et al., 2009), and LL_f can therefore be represented as the sum of the time of leaf growth (LL_g), during which the P_a increases to reach a maximum, and the time of leaf senescence (LL_s), during which the P_a decreases to reach a value of zero:

$$LL_f = LL_g + LL_s. \quad (3)$$

The entire LL can then be represented by a sum of three components:

$$LL = LL_g + LL_s + LL_n. \quad (4)$$

Changes in the conductivity of leaf tissue for CO_2, the content of chlorophyll and soluble protein, and the activity of RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase) during leaf ontogeny follow the same pattern as P_a (Friedrich and Huffaker, 1980; Makino et al., 1983; Suzuki et al., 1987; Wilson et al., 2001; Warren, 2008). Moreover, P_a itself follows the same pattern over the daylight hours and the vegetation period in the boreal zone, clearly adjusting to the changes in solar radiation (Hari and Mäkelä, 2003; Ibrom et al., 2006).

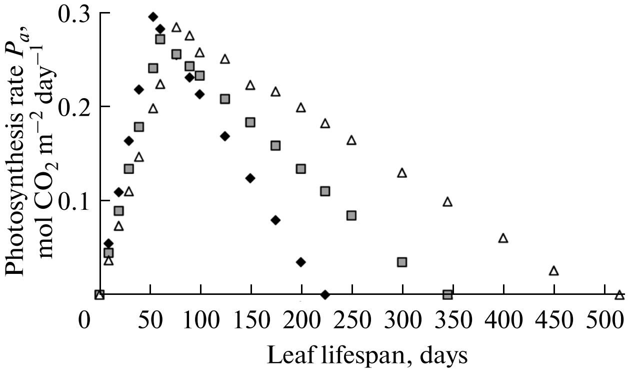

Fig. 2. Changes in the rate of photosynthesis during the ontogeny of leaves with different lifespans. Legend: diamonds—*Bischofia javanica* Blume (LL = 224 days), squares—*Gordonia axillaris* Dietr (LL = 345 days), triangles—*Machilus japonica* J.C. Liao (LL = 515 days). According to (Kuo et al., 2009) with the author's modifications.

The amount of CO_2 fixed over the lifetime of the leaf is defined by an integral of the dP_a/dt function at t values ranging from 0 to LL_f. The integral value corresponds to the area under the curve determined by the function. The area under the curve can be considered triangle-shaped for a first approximation (Fig. 2). Thus, the amount of CO_2 fixed over the lifetime of the leaf (LL_f) corresponding to the photosynthetic potential of the leaf can be determined according to the equation

$$PPL = LL_f\,P_{a\,\max}/2, \quad (5)$$

or equation (1),

$$PPL = LMA \cdot LL_f\,P_{m\,\max}/2. \quad (6)$$

The $P_{a\,\max}/2$ ($P_{m\,\max}/2$) parameter of these equations represents the average rate of photosynthesis during its functioning. The PPL parameter characterizes the maximal possible amount of CO_2 fixed by the leaf over its lifespan. The parameters have the following dimensions: PPL, mol CO_2 m^{-2}; $P_{a\,\max}$, mol CO_2 m^{-2} day^{-1}; LL_f, days; $P_{m\,\max}$, mol CO_2 g^{-1} day^{-1}; and LMA, g m^{-2} (g of dry mass). The average duration of the daylight period during LL_f must be determined in order to calculate $P_{a\,\max}$. It is nearly 12 h over the whole year in the equatorial zone, while in other cases it depends on the latitude of the site where the plants grow. As the LL_f decreases and the distance between the equator and the habitat of a plant increases, an accurate definition of the daylight period duration becomes increasingly important, especially in the case of ephemeric species characterized by a short lifespan of the leaf.

Changes in P_a over the daylight period under natural conditions (in situ illumination) are characterized by a curve similar to that characterizing P_a dynamics throughout the ontogenesis of the leaf, and therefore

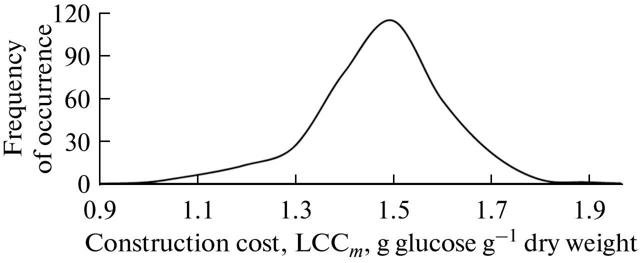

Fig. 3. Distribution of construction cost per unit dry weight of the leaf (LCC_m) for 322 plant species. According to (Baruch and Goldstein, 1999; P'yankov et al., 2001; Villar and Merino, 2001; Navas et al., 2003; Kikuzawa and Lechowicz, 2006; and Osunkoya et al., 2008).

the amount of CO_2 fixed within one day is calculated similarly to PPL by the following equations:

$$P_{a\,\max} = tP_a/2, \tag{7}$$

$$P_{m\,\max} = tP_m/2, \tag{8}$$

where t is the average number of hours per photoperiod in the LL_f range. The dimensions of parameters in these equations are the following: P_a, mol CO_2 m^{-2} h^{-1}; P_m, mol $CO_2 g^{-1} h^{-1}$, and t, h.

The dP_a/dt function used to determine the PPL value is analogous to acceleration in mechanics. The biological significance of this acceleration can be defined as the rate of PPL realization (RR PPL). RR PPL is a scalar value calculated according to the equation:

$$\text{RR PPL} = 2P_{a\,\max} : LL_f. \tag{9}$$

If the leaf age at which $P_a = P_{a\,\max}$, and thus the LL_g value, is known, the rate of PPL realization during growth (RR PPL_g) and senescence (RR PPL_s) of the leaf can be calculated:

$$\text{RR PPL}_g = P_{a\,\max} : LL_g, \tag{10}$$

$$\text{RR PPL}_s = P_{a\,\max} : LL_s. \tag{11}$$

The dimension of RR PPL is (mol CO_2 m^{-2} day^{-2}). RR PPL characterizes the average rate of photosynthetic potential consumption during the period of active leaf functioning.

Thus, the photosynthetic potential of the leaf is the CO_2 amount that can potentially be fixed by the leaf during its lifetime; this amount is defined as the product of the average rate of photosynthesis and the number of days of photosynthesis. The rate of realization of the photosynthetic potential is defined as the ratio of the doubled maximal rate of photosynthesis to the number of days of photosynthesis and characterizes the rate of photosynthesis rate change during leaf ontogenesis. The nonfunctional longevity of the leaf (LL_n) does not affect the photosynthetic potential. Species with a higher LL_f will have a higher PPL if the $P_{a\,\max}$ for this species is the same or higher than in the species used for comparison.

CONSTRUCTIONAL COST AND PAYBACK OF THE LEAF

The construction cost (the amount of glucose consumed during the synthesis of 1 g of the final product of a biological system) reflects the productivity of biosynthetic processes as the ratio of the amounts of the substrate and the final product (Penning Vries, et al., 1974). The leaf construction cost LCC_m is expressed in grams of glucose per 1 g dry weight (Poorter et al., 2006). The variability of this parameter is low, with 20 of the 26 plant species listed in (Kikuzawa and Lechowicz, 2006) having almost the same LCC_m value (1.5). The LCC_m values for 260 plant species of different life forms and habitats varied in a narrow range of 1.0–1.9 (Baruch and Goldstein, 1999; P'yankov et al., 2001; Villar and Merino, 2001; Navas et al., 2003; Kikuzawa and Lechowicz, 2006; Osunkoya et al., 2008). The distribution of interspecies variability of this parameter was close to normal, with an arithmetic mean of 1.5 (Fig. 3). The low level of LCC_m variation among species makes it possible to use the average LCC_m value as a constant for all leaves of higher plants (for a first approximation).

The leaf construction cost LCC_a, i.e., the amount of glucose required for the production of dry mass per unit leaf area (LMA) varies considerably between species (Villar and Merino, 2001) due to the considerable interspecies variability of LMA (Wright et al., 2004) that connects LCC_a and LCC_m as shown by the equation (1):

$$LCC_a = LCC_m \text{LMA}. \tag{12}$$

The LCC_a dimension is (g glucose m^{-2} of leaf area).

The leaf payback (LP) can be defined as the ratio of the construction cost LCC_a to the photosynthetic potential PPL and expressed as a percentage:

$$\text{LP} = (LCC_a : \text{PPL}) \times 100\%. \tag{13}$$

This parameter characterizes the mass fraction of CO_2 assimilated during the lifetime of the leaf, and its value is equal to LCC_a. The LP parameter expressed in percent is equally applicable to unit leaf area and the whole leaf. This approach requires the parameters used to be of the same dimension. The dimension of P_a is (mol CO_2), and that of LCC_m is (gram glucose), and therefore it is necessary to define the relationships between grams glucose and mols of CO_2. LCC_a was expressed in mol CO_2 m^{-2} in (Oikawa et al., 2006). The dimensions can be interconverted using the well-known general equation describing photosynthesis:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2. \tag{14}$$

Simple calculations show that the average LCC_m of 1.5 g glucose g^{-1} dry weight is equivalent to 2.2 g CO_2 g^{-1} dry weight or 0.05 mol CO_2 g^{-1} dry weight. The conversion of glucose weight into the CO_2 amount performed by other authors yielded a conversion factor of 1/30 as well (Oikawa et al., 2006). In this case, equation (7) can be transformed in the following way:

Table 1. Functional characteristics of leaves of three tree species from Taiwan

Parameters	Species		
	Bischofa javanica Blume, deciduous	*Gordonia axillaris* Dietr., evergreen	*Machilus japonica*, J.C. Liao, evergreen
LL = LL_f, days	224 ± 7	345 ± 21	515 ± 28
LL_g, days	54 ± 8	61 ± 9	77 ± 6
LL_s, days	170 ± 5	284 ± 17	438 ± 24
LMA, g m^{-2}	70 ± 3	84 ± 10	173 ± 7
LCC_a, mol CO_2 m^{-2}	3.5 ± 0.2	4.2 ± 0.5	8.7 ± 0.3
$P_{a\,\max}$, mol CO_2 m^{-2} day^{-1}	0.30 ± 0.01	0.27 ± 0.01	0.29 ± 0.06
$P_{m\,\max}$, $\times 10^{-3}$ mol CO_2 g^{-1} day^{-1}	4.29 ± 0.14	3.21 ± 0.11	1.68 ± 0.33
PPL, mol CO_2 m^{-2}	33 ± 1	47 ± 3	74 ± 4
LP_t, days	23 ± 1	31 ± 4	60 ± 2
LP, %	11 ± 1	9 ± 1	12 ± 1
RR PPL_g, $\times 10^{-3}$ mol CO_2 m^{-2} day^{-1}	5.5 ± 0.2	4.5 ± 0.3	3.7 ± 0.2
RR PPL_s, $\times 10^{-3}$ mol CO_2 m^{-2} day^{-1}	1.8 ± 0.1	1.0 ± 0.1	0.7 ± 0.1
RR PPL, $\times 10^{-3}$ mol CO_2 m^{-2} day^{-1}	2.7 ± 0.1	1.6 ± 0.1	1.1 ± 0.1

Length of the day is 12 hours, $n = 11$. According to (Kuo et al., 2009) with the author's modifications.

$$LCC_a = 0.05\text{LMA (mol CO}_2\text{ m}^{-2}). \quad (15)$$

Equations 7 and 10 imply that all relationships between LMA and other parameters of the leaf are valid for LCC_a as well. The reliability of this approach is confirmed by the existence of a strong positive correlation between LMA and LCC_a, but not between LMA and LCC_m (Coste et al., 2011).

Leaf payback time (LP_t) characterizes the number of days of photosynthesis required for the assimilation of a CO_2 amount equal to the construction cost LCC_a at an average photosynthesis rate ($P_{a\,\max}/2$). LP_t can be calculated by the equations:

$$LP_t = 2LCC_a : P_{a\,\max}, \quad (16)$$

$$LP_t = 0.1\text{LMA} : P_{a\,\max}, \quad (17)$$

$$LP_t = 0.1 : P_{m\,\max}. \quad (18)$$

The maximal photosynthesis rate is expressed in mol CO_2 m^{-2} day^{-1} and mol CO_2 g^{-1} day^{-1}, and leaf payback time is expressed in days in these equations. The LP_t parameter can be used to calculate the LP value

$$LP = (LP_t : LL_f) \times 100\%. \quad (19)$$

In expression (19), LP characterizes the ratio between the number of days of active photosynthesis during which the amount of CO_2 equal to the construction cost LCC_a is assimilated and the total functional lifetime of the leaf.

ASSESSMENT OF FUNCTIONAL PARAMETERS OF THE LEAVES OF DECIDUOUS AND EVERGREEN SPECIES

The approach described above has been used to calculate the values of the leaf functional parameters: LL_f, LCC_a, PPL, RR PPL, LP_t, and LP in deciduous (LL less than one year) and evergreen (LL more than one year) arboraceous plants, both gymnosperms (conifers) and angiosperms (mostly dicotyledonous). The values used in the calculations (LL, LMA, and P_a or P_m) were taken from published reports (Reich et al., 1999; Lusk et al., 2003; Kitajima et al., 2005; Santiago and Wright, 2007; Fujita et al., 2012). Trees predominated among the species chosen for analysis, since this allowed for reliable comparison of species from different habitats; however, several bush species were considered as well. Deciduous species (48 of the angiosperm species) from five habitats, 40 evergreen angiosperm species from four habitats, and 23 coniferous species from two habitats were analyzed. The average length of the daylight period during the growing season was assumed to be 12 hours for the latitude range of 2°–9°, 13 hours for 30°–35°, and 14 hours for 37°–43°.

Moreover, data for three angiosperm species (one deciduous and two evergreen) growing in Taiwan (23° N) reported in (Kuo et al., 2009) were analyzed in the present work. These data form a detailed characteristic of the dynamics of the maximal rate of photosynthesis during leaf ontogenesis in each species, with two minima close to zero and a single maximum ($P_{a\,\max}$). The leaf age LL_g corresponding to the maximal photosynthesis rate was reported for each species, which provided an opportunity to calculate the time of leaf senescence LL_s (Table 1). The $P_{a\,\max}$ values for different species were almost identical, regardless of the dramatic differences between the LL values (Table 1), i.e., $P_{a\,\max}$ did not depend on LL. Leaves of different species attained $P_{a\ \max}$ at different ages (Table 1), and LL_g was higher in leaves with higher LL values. This allows for the assumption of a slower photosynthesis system formation and "maturation" of chloroplasts in species with longer LL. Leaf senescence periods LL_s were longer in species with higher LL values as well (Table 1), which is in accordance with the widely accepted concept of comparable times of leaf growth and formation in deciduous and evergreen species with a several year-long leaf senescence period in the latter species (Mokronosov, 1981). Chloroplast "aging" is apparently slower in leaves with longer lifespans. The leaf age LL_g corresponding to the maximal photosynthesis rate $P_{a\ \max}$ significantly exceeded the age of complete unfolding of the leaves (Kuo et al., 2009); the difference is greater in species with longer LL (27, 38, and 58 days, respectively) (Table 1). Chloroplast formation in arboraceous species is assumed to continue after the completion of leaf surface expansion: for instance, the development of chloroplasts in the evergreen species *Castanopsis sieboldii* Makino was completed 15–40 days later than stabilization of the leaf area (Miyazawa and Terashima, 2001). This fact indicates a probable discrepancy between the moment of complete leaf unfolding and that of completion of chloroplast formation corresponding to maximal P_a; the discrepancy is assumed to be especially pronounced in species with longer LL. The LL_g value can be considered the age of leaf "maturation."

An increase of the total leaf longevity ($LL = LL_f$), the period of leaf growth and formation (LL_g), the period of leaf senescence (LL_s), dry weight of the leaf per unit area (LMA), construction costs per unit area (LCC_a), photosynthetic potential of the leaf (PPL) and leaf payback time (LP_t) was accompanied by a decrease of $P_{m\ \max}$, RR PPL_g, RR PPL_s, and RR PPL, while $P_{a\ \max}$ and LP remained almost the same (Table 1) (Kuo et al., 2009). The low variability of $P_{a\ \max}$ demonstrated that the increase of PPL and LP_t in the analyzed species was due to increases in LL and LCC_a, respectively. The simultaneous increase of LCC_a and PPL led to stabilization of leaf payback LP (Table 1). The photosynthesis rate $P_{m\ \max}$ decreased significantly upon an increase of LL and a virtually unchanged $P_{a\ \max}$ (Table 1), which is evidence of underestimation of photosynthesis rate associated with use of the P_m parameter. The underestimation became more pronounced as LL increased. A decrease of RR PPL_g and RR PPL_s associated with an increase of LL may be an indirect indication of a decrease of chloroplast formation rate and aging of the leaf.

Let us consider the variability of the functional characteristics of the leaf in a greater number of species (Table 2) analyzed in published studies (Reich et al., 1999; Lusk et al., 2003; Kitajima et al., 2005; Santjago and Wright, 2007; Fujita et al., 2012). A significant increase of LL and LL_f in the series of deciduous angiosperms → evergreen angiosperms → evergreen gymnosperm conifers (DA → EGA → EGGC) was accompanied by increases in LMA, LCC_a and LP_t, while $P_{m\ \max}$ and RR PPL decreased. This is consistent with the data presented in Table 1. Analysis of a larger group of species showed that the photosynthesis rate $P_{a\ \max}$ decreased significantly as LL and LL_f increased (Table 2). This is consistent with the reported decrease of both types of photosynthesis rate (P_a and P_m) concomitantly with an increase of the overall leaf longevity (Reich et al., 1992). The decrease of $P_{m\ \max}$ concomitant to the increase of LL was much more (almost twice more) pronounced than the corresponding decrease of $P_{a\ \max}$ for the species analyzed in the present work (Table 2). LCC_a and $P_{a\ \max}$ were not correlated within each range of species, while a significant negative correlation was observed for LCC_a and $P_{m\ \max}$ (Fig. 4a and 4b). This result is consistent with the lack of correlation between LMA and $P_{a\ \max}$ and a negative correlation (–0.7) between LMA and $P_{m\ \max}$ demonstrated for a large group of species (Wright et al., 2004). Why is the photosynthesis rate $P_{m\ \max}$, but not $P_{a\ \max}$, correlated to LMA and LCC_a? $P_{a\ \max}$ corresponds to the actual photosynthesis rate, i.e., the amount of CO_2 fixed per unit time by a part of the leaf with a certain area, while $P_{m\ \max}$ corresponds to the relative photosynthesis rate, since it is defined as $P_{a\ \max}$ divided by LMA (Equation (1)). However, the dry mass used to determine LMA and the entire leaf mass was previously shown to be inhomogeneous (Vasfilov, 2011), since it reflects the total mass of all protoplasts linked by plasmadesmata to form a continuous network (symplast) added to the total mass of all cell walls. Chloroplasts, which mediate photosynthesis, are located in the symplast; the photosynthesis rate P_m is therefore always underestimated, since the dry mass of the cell walls is taken into account. The underestimation becomes more pronounced as the mass of cell walls in the leaf (and consequently, the LMA value) increases (Vasfilov, 2011). The variability of cell wall dry mass may underlie the 1.5-fold greater variability of $P_{m\ \max}$ within each group of species as compared to $P_{a\ \max}$ (Table 2). The cell walls play an important role in maintaining the mechanical strength of the plants, which is especially important for long-lived leaves (Terashima et al., 2001). The increase of LMA, LCC_a, LL, and LL_f in the DA → EGA → EGGC range and the concomitant P_m decrease, which is more pronounced than that of P_a, can be interpreted as a sign of more advanced apoplast development in leaves with a longer lifespan.

Estimation of P_m as the ratio of P_a to the dry mass of all chloroplasts (with starch excluded) with consideration of the symplast component mediating photosynthesis yields a nearly constant P_m with very low interspecies variability contrasting with that of P_a. This P_m can be regarded as the photosynthesis rate of a sin-

Table 2. Functional characteristics of the leaf in angiosperm and gymnosperm coniferous tree species from different habitats

Parameters	Angiosperms				Gymnosperms, coniferous	
	deciduous		evergreen		evergreen	
	habitat latitudes					
	2°, 9°, 33°–43° N		2°, 9°, 30° N 37°–41° S		33°–43° N 37°–41° S	
	Average annual temperature, precipitation and altitude over sea level					
	8–27°C 222–4477 mm, 3–1890 m		9–26°C 1300–4477 mm, 5–1200 m		−3…+18 × C 222–1850 mm, 3–3510 m	
	Number of species (sample size)					
	47 (58)		38 (58)		23 (25)	
	$M \pm m$	CV, %	$M \pm m$	CV, %	$M \pm m$	CV, %
LL, days	193 ± 9	34	756 ± 46	46	1388 ± 137	48
LL_f, days	193 ± 9	34	652 ± 44	51	861 ± 75	42
LMA, g m^{-2}	91 ± 4	35	126 ± 5	28	220 ± 17	38
LCC_a, mol $\mathrm{CO_2\ m^{-2}}$	4.6 ± 0.2	35	6.3 ± 0.2	28	11.0 ± 0.8	38
$P_{a\,\max}$, mol $\mathrm{CO_2\ m^{-2}\ day^{-1}}$	0.28 ± 0.01	26	0.22 ± 0.01	26	0.16 ± 0.01	32
$P_{m\,\max}$, $\times10^{-3}$ mol $\mathrm{CO_2\ g^{-1}\ day^{-1}}$	3.43 ± 0.19	43	1.87 ± 0.10	38	0.88 ± 0.09	53
PPL, mol $\mathrm{CO_2\ m^{-2}}$	26 ± 1	39	65 ± 3	38	70 ± 7	53
LP_t, days	35 ± 2	45	64 ± 4	44	155 ± 20	64
LP, %	18 ± 1	45	11 ± 1	34	20 ± 2	58
RR PPL, $\times10^{-3}$ mol $\mathrm{CO_2\ m^{-2}\ day^{-1}}$	3.33 ± 0.28	63	0.88 ± 0.07	58	0.47 ± 0.06	62

According to (Reich et al., 1999; Lusk et al., 2003; Kitajima et al., 2005; Santjago and Wright, 2007; and Fujita et al., 2012) with the author's modifications.

gle average chloroplast (for a first approximation), i.e., the benchmark rate of photosynthesis measured under standard conditions. The absence of correlation between $P_{m\,\max}$ and $P_{a\,\max}$ can be expected in this case. However, the correlation was 0.7 ($r^2 = 0.49$, $p < 0.001$) for the composite sample of three groups of species considered in the present work (Table 2). The same correlation with a different sign (−0.7) was reported for LMA and P_m values determined in 700 species (Wright et al., 2004); therefore, the absence of a relationship between these two correlations and photosynthesis can be expected.

The PPL variability between groups of species was not unidirectional (Table 2). The value for deciduous species was approximately 2.5 times lower than that for the evergreen species, and the values for angiosperm and conifer evergreen species are virtually similar. The low PPL values in deciduous species were largely due to the fact that LL_f was significantly lower in these species than in evergreen conifers and angiosperms (3.4 and 4.5 times lower, respectively) (Table 2). The contribution of the LL_f parameter to PPL was much greater than that of $P_{a\,\max}$. There was either no positive correlation or a weak correlation between PPL and $P_{a\,\max}$, while the correlation between PPL and LL_f was strong within each group of species (Fig. 4c and 4d). This is consistent with the data presented in Table 1. The average $P_{a\,\max}$ for deciduous species (Table 2) was virtually identical to that of the three species listed in Table 1. Average $P_{a\,\max}$ values decreased, while LL and LL_f values increased upon the transition from deciduous to evergreen angiosperms and further to evergreen conifers (Table 2). $P_{a\,\max}$ and LL_f were not correlated in deciduous species, while a negative correlation ($r = -0.52$, $r^2 = 0.27$, $p < 0.001$) was demonstrated for the combined group of evergreen species. This correlation illustrated the trend towards decreased $P_{a\,\max}$ concomitant with increased LL_f in evergreen species, i.e., in species with a long LL. One of the reasons for the detection of this trend may be the time point selection for the measurement of $P_{a\,\max}$: as a rule, the measurements were performed in leaves grown to final size. The time required for the completion of the photosynthetic system formation and $P_{a\,\max}$ attainment after the completion of leaf growth was shown to be longer in species with longer

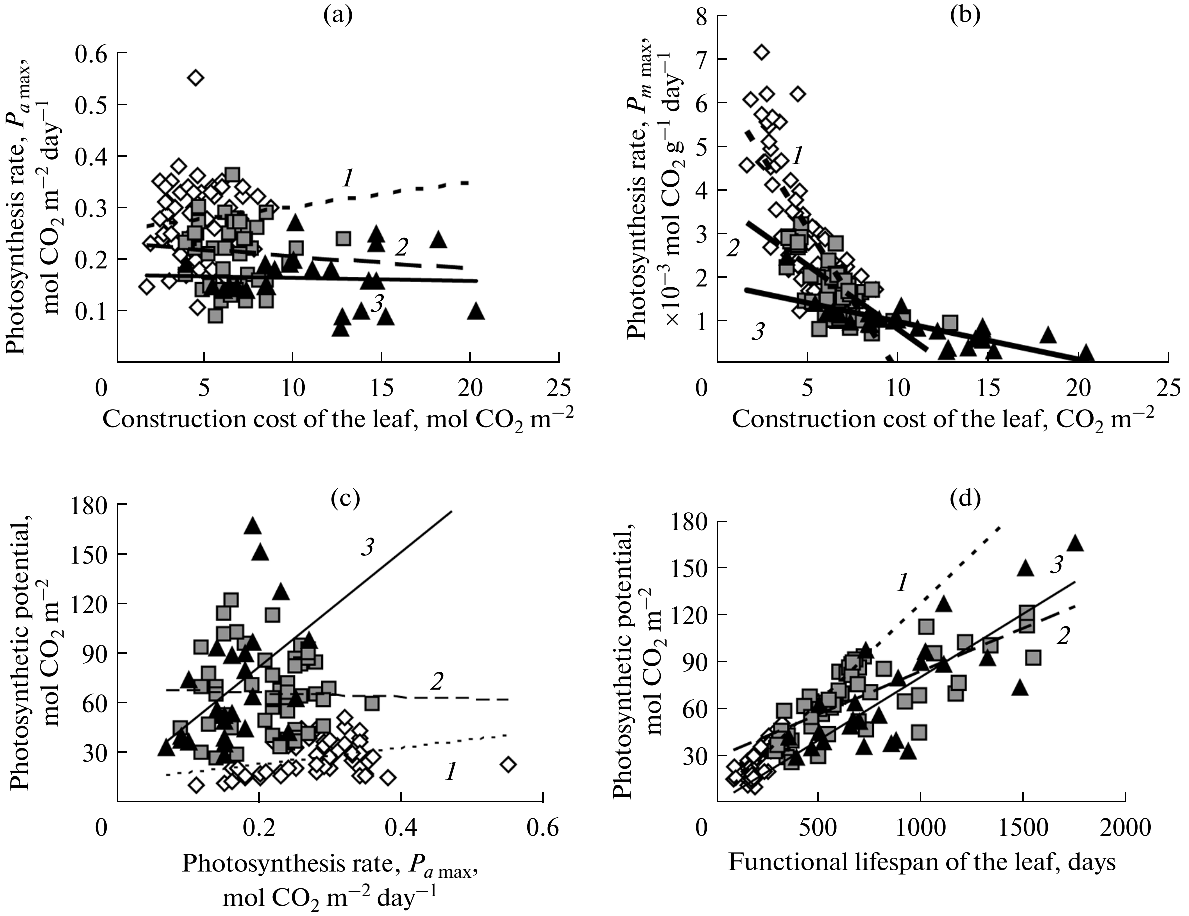

Fig. 4. Relationships between the construction cost of the leaf LCC_a and photosynthetic rate $P_{a\,\max}$ (a) or $P_{m\,\max}$ (b), and the relationships between the photosynthetic potential PPL and photosynthesis rate $P_{a\,\max}$ (c) or the functional leaf lifespan LL_f (d). Symbols: diamonds (*1*) deciduous angiosperm species; gray squares (*2*) evergreen angiosperm species; black triangles (*3*) evergreen conifer gymnosperm species. Correlation coefficients: (a) (*1*) $r = 0.1$, not significant; (*2*) $r = -0.08$, not significant; (*3*) $r = -0.05$, not significant. (b) (*1*) $r = -0.74$, $r^2 = 0.55$, $p < 0.001$; (*2*) $r = -0.72$, $r^2 = 0.52$, $p < 0.001$; (*3*) $r = -0.78$, $r^2 = 0.61$, $p < 0.001$. In (c) (*1*) $r = 0.37$, $r^2 = 0.14$, $p < 0.01$; (*2*) $r = -0.03$, not significant; (*3*) $r = 0.48$, $r^2 = 0.23$, $p < 0.05$. (d) (*1*) $r = 0.81$, $r^2 = 0.66$, $p < 0.001$; (*2*) $r = 0.77$, $r^2 = 0.59$, $p < 0.001$; (*3*) $r = 0.79$, $r^2 = 0.62$, $p < 0.001$. According to (Reich et al., 1999; Lusk et al., 2003; Kitajima et al., 2005; Santjago and Wright, 2007; and Fujita et al., 2012) with the author's modifications.

LL (Kuo et al., 2009). Therefore, underestimation of $P_{a\,\max}$ in evergreen species (Table 2) appears possible, and the actual average value for these species are presumably close to the average value for deciduous species.

RR PPL, rather than PPL, determines the growth rate of a plant. A rather strong positive correlation existed between $P_{a\,\max}$ and RR PPL in each group of species, while the correlation between LL_f and RR PPL within the groups was negative (Fig. 5a and 5b). Calculation of these parameters based on data reported in (Kitajima et al., 2002) showed that the LL in a fast-growing pioneer species *Cecropia longipes* Pitt. characteristic of early succession stages was twice lower than in species characteristic of late succession stages, while $P_{a\,\max}$ for the former species was 2.5 times higher, RR PPL was 5 times higher, and the PPL values were similar. Thus, higher RR PPL values are associated with lower LL values and higher plant growth rates.

The increase of leaf payback time (LP_t) in groups of species was associated with an increase in LMA (LCC_a) and LL (LL_f) (Table 2). However, the positive correlation between leaf payback time LP_t and the construction cost LCC_a ($r = 0.83$, $r^2 = 0.69$, $p < 0.001$) was more pronounced than that between LP_t and functional leaf lifespan LL_f ($r = 0.56$, $r^2 = 0.31$, $p < 0.001$). This implies a weak dependence of LP_t on PPL. Indeed, the correlation between LP_t and PPL for the three groups of species was very weak ($r = 0.23$, $r^2 = 0.05$, $p < 0.01$), and no correlation could be detected within each group of species (Fig. 5c). The dependence of LP_t on RR PPL was weak as well, with

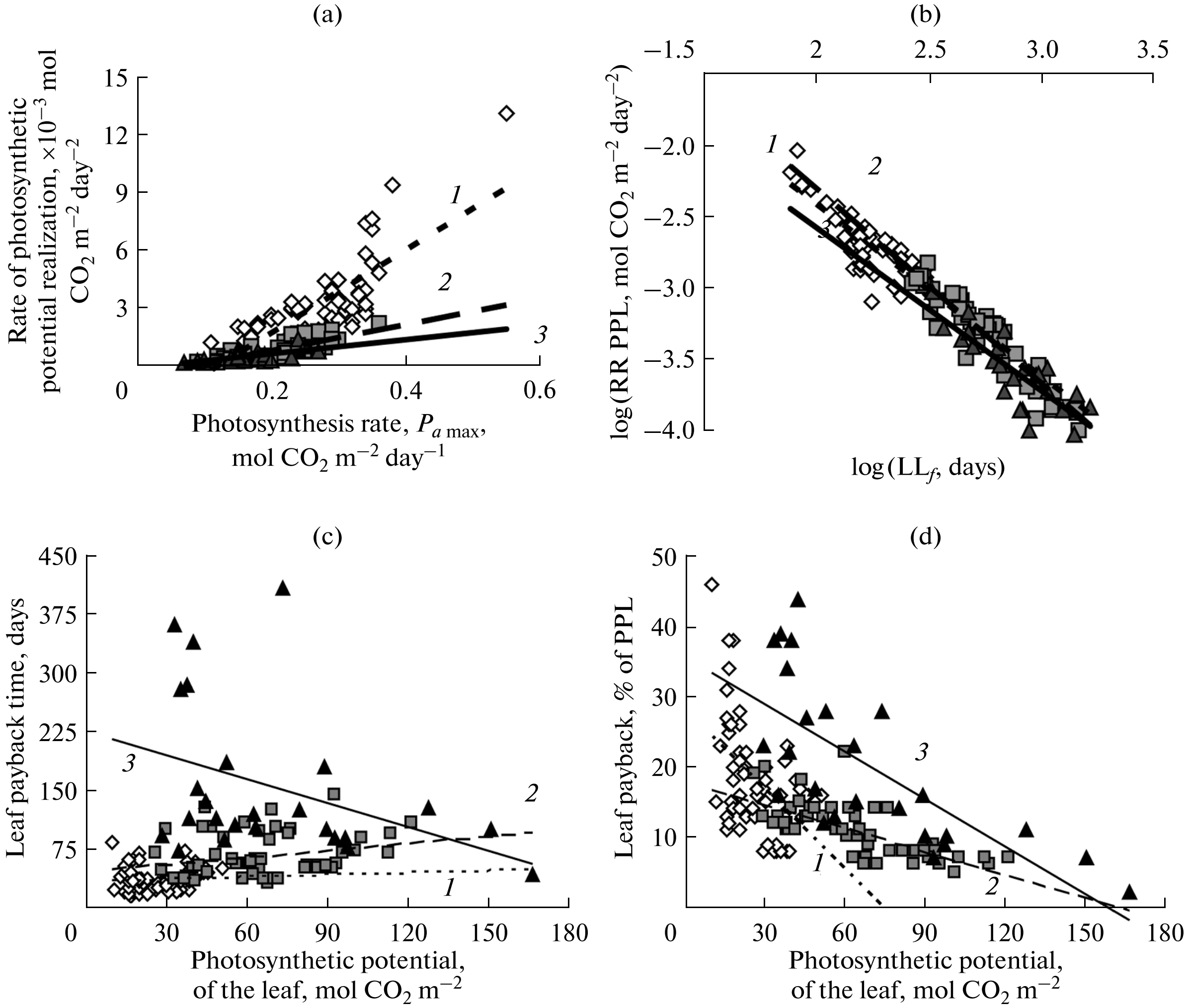

Fig. 5. Relationships between the rate of realization of the photosynthetic potential of the leaf (RR PPL) and the rate of photosynthesis $P_{a\ \max}$ (a) or the functional lifespan of the leaf (LL_f) (both values log-transformed) (b), and relationships between the photosynthetic capacity of the leaf (PPL) and leaf payback time (LP_t) (c) or leaf payback (LP) (d). Symbols are the same as in Fig. 4. Correlation coefficients: (a) (*1*) $r = 0.76$, $r^2 = 0.58$, $p < 0.001$; (*2*) $r = 0.75$, $r^2 = 0.56$, $p < 0.001$; (*3*) $r = 0.65$, $r^2 = 0.42$, $p < 0.001$. (b) (*1*) $r = -0.83$, $r^2 = 0.69$, $p < 0.001$; (*2*) $r = -0.94$, $r^2 = 0.88$, $p < 0.001$; (*3*) $r = -0.82$, $r^2 = 0.67$, $p < 0.001$. (c) (*1*) $r = 0.06$, not significant; $r = 0.26$, not significant; $r = -0.38$, not significant. (d) (*1*) $r = -0.48$, $r^2 = 0.23$, $p < 0.001$; (*2*) $r = -0.7$, $r^2 = 0.49$, $p < 0.001$; (*3*) $r = -0.72$, $r^2 = 0.52$, $p < 0.001$. According to (Reich et al., 1999; Lusk et al., 2003; Kitajima et al., 2005; Santjago and Wright, 2007; and Fujita et al., 2012), with the author's modifications.

the correlation between these two parameters amounting to $r = -0.45$ ($r^2 = 0.2$, $p < 0.001$), and therefore one can assume that LP_t increase concomitant to the increase of LL in a group of species is not related to variability of the photosynthesis system, but rather to an increase in cell wall mass in the same direction. A distinct decrease of P_m but not P_a in the same direction speaks in favor of the hypothesis presented above.

The positive correlation between LP and LCC_a for the three groups of species was virtually nonexistent ($r = 0.37$, $r^2 = 0.14$, $p < 0.001$), in contrast to that between LP_t and LCC_a ($r = 0.83$). A distinct negative correlation between LP and PPL was more pronounced in both groups of evergreen species than in deciduous species, which is in accordance to PPL and LL_f variation in the groups of species (Fig. 5d, Table 2). This is due to a more pronounced dependence of PPL on LL_f. Thus, the dependence of LP on PPL is more pronounced than the dependence on LCC_a (and consequently, on LL_f), in contrast to the dependence of LP_t on these parameters.

Leaf payback (LP) in deciduous angiosperm species was similar to the respective parameter of evergreen conifer species and significantly higher than that of the evergreen angiosperm species (Table 2); LP for the latter group of species was virtually the same as in three species listed in Table 1. Leaf payback ranged from 2 to 46% (Fig. 5d), i.e., LP did not exceed 50% of either PPL or LL_f. LP_t was shown to be lower than half LL in a range of herb and tree species, both deciduous and evergreen (Poorter et al., 2006), i.e., payback did not exceed 50% in this group of species either. Payback ranged from 5 to 23% (with an average value of 14%) for the major part (86%) of the sample for all three groups of species, while the average value for the entire sample was 15%. LP variability within the group of evergreen angiosperm species was 1.5 times lower than in the other two groups (Table 2), and therefore one can assume that the average LP for the studied species is approximately 11% of PPL. Indeed, the LP ranged from 5 to 17% in 70% of species in the entire sample, the average value being 11%. The changes in LMA and LCC_a were obviously unidirectional, as well as those of LL and LL_f, while the LP values for the three groups of species, including deciduous species and evergreen conifers, were almost identical, notwithstanding the dramatic differences between the characteristics of the species. Therefore one can assume that unidirectional changes of these parameters stabilize the LP and LCC_a increase is not accompanied by an increase in LP. This is due to the simultaneous increase of LCC_a and LL_f; the latter parameter has a significant effect on PPL. The relative stability of LP is probably due to interspecies and intraspecies competition for environmental resources affecting photosynthesis, as well as to the competition for these resources among the leaves of an individual plant. The assumption of unidirectional LMA and LL changes providing competitive advantages for the species due to reduced leaf payback (Reich et al., 1997; Wright et al., 2004; Falster et al., 2012; Westoby et al., 2013) can therefore be doubted, although it was derived from the analysis of several parameters from the spectrum of leaf economy (LCC_m, LL, LMA, P_a, and P_m). The results of the present work imply that the competition among leaves within an individual, within a species, and between species, is directed towards the stabilization of leaf payback. LP stabilization implies the existence of an optimal LP value. The selection for optimal leaf payback is supposedly mediated by an increase in photosynthesis rate and the total lifespan of the leaf (Blonder et al., 2011); however, the present study showed that the interspecies variability of $P_{a\ \max}$ is significantly lower than that of LL, and therefore a connection between the selection underlying LP optimization and the increase of photosynthesis rate is unlikely to exist, given that the photosynthesis rate is constantly changing during leaf ontogenesis. The results of the present work show that the optimal value of leaf payback is approximately 11% of PPL.

Thus, the unidirectional changes in LMA, LCC_a, LL and LL_f for individual species are inversely proportional to $P_{m\ \max}$ and RR PPL changes, while LP varies only slightly. Unidirectional changes of PPL and LCC_a stabilize the LP. The average LP in the studied species amounted to 14% of PPL, while the optimal LP may be close to 11% of PPL. The construction cost and longevity of the leaf have almost no effect on leaf payback. LL_f has a stronger effect on the PPL value than $P_{a\ \max}$; the longer LL_f of evergreen species gives them an advantage, a higher PPL than in deciduous species in case of $P_{a\ \max}$ values for deciduous and evergreen species being comparable. The rate of PPL implementation determines the lifespan of the leaf, with lower rates characteristic of longer-lived leaves.

LEAF LIFESPAN AND PHOTOSYNTHESIS

Slow metabolism is associated with a longer leaf lifespan (Reich et al., 2007; Simonin et al., 2012). Photosynthesis is one of the main components of leaf metabolism, and therefore LL can be expected to depend on environmental factors that affect the rate of photosynthesis. As a factor changes to promote increased P_a, a decrease in LL takes place, and if P_a decreases, LL increases. RR PPL characterizes the average rate of P_a change over the lifetime of the leaf. Changes in RR PPL obviously show a positive correlation with metabolic activity in the leaf. RR PPL is not affected by the LL_n value, while there is an inverse proportionality between RR PPL and LL_f (Equation (9)). The coefficient of correlation between LL_f and LL in the species investigated (Table 2) was $r = 0.9$ ($r^2 = 0.81$, $p < 0.001$), and therefore the variability of LL and LL_f can be used as a first-approximation characteristic of the variability of PPL and RR PPL. For example, the LL of pine needles in the better illuminated upper part of the tree crown is greater and the P_a is higher than those of the genotypically identical needles in the lower part of the crown (Sudachkova et al., 1990; Warren and Adams, 2001; Vasfilov, 2005; Niinemets et al., 2007), which implies the dependence of the LL value on the activity of photosynthesis, one of the components of leaf metabolism. Therefore, one can expect a higher rate of identical PPL realization in the better illuminated upper part of the tree crown as compared to the lower part of the crown. Mutations affecting photosynthesis and metabolism affect the LL as well: for example, the ore4-1 mutation affecting one of chloroplast ribosomal proteins of *Arabidopsis thaliana* ((L.) Heynh.) reduces the rates of growth, photosynthesis, and metabolism, and increases the LL (Woo et al., 2002).

Light has a positive effect on P_a, the nitrogen content, and RuBisCO but a negative effect on LL (Evans and Poorter, 2001; Reich et al., 2004; Vincent, 2006). An increase in illumination, P_a, and RR PPL is expected to be associated with a decrease in LL. Such an association is observed in heliophytes and shade-tolerant species that show a higher P_a at a lower LL in well-illuminated habitats as compared to shadowy habitats (Valladares et al., 2000; Hikosaka, 2010). A significant increase in illumination blocks photosynthesis in scyophytes at the level of stomata: for example, the stomata of coffee (*Coffea arabica* L.) are closed immediately after the leaves become exposed to direct sunlight, i.e., after a sharp increase in luminance (Walter, 1968). This phenomenon of RR PPL reduction underlies leaf lifespan increase in scyophytes. RR PPL decreases in the series of heliophytes → shade-tolerant species → scyophytes, while LL increases in the same order.

A water deficit reduces stomatal conductance and photosynthesis rate (Muller et al., 2011). It is accompanied by a decrease in RR PPL and an increase in LL. As a critical level of water deficit is achieved, the leaf can either fall (in deciduous species) or assume a resting state (in evergreen species). RR PPL and LL changes in aquatic plants not exposed to water deficit are evoked by changes in irradiation and temperature. Thus, the LL for zostera (*Zostera marina* L.) depended on illumination only weakly, while a decrease in water temperature induced a 2.5-fold increase in LL (Hosokawa et al., 2009). This is due to the negative impact of low temperature on the rate of metabolite transport and plant growth. A decrease in temperature is usually accompanied by a decrease in the rates of respiration and metabolism and an increase in LL. LL_n, a period when photosynthesis does not occur, accounts for the LL increase in boreal evergreen species.

The rate of water transport, and hence the rate of metabolite transport, is positively correlated to the rate of photosynthesis and growth and negatively correlated to LL (Ren et al., 2011; Pantin et al., 2012). Low temperatures inevitably lead to inhibition of the growth and transport of photosynthesis products, accumulation of sugars in the leaf, and repression of photosynthetic genes (Boonman et al., 2009; Sheen, 2010). Consequently, P_a and RR PPL decrease and LL increases, which is typical for species advancing towards the north and for plants exposed to environmental conditions pessimal for growth (Starostin, 1974; Walter, 1973; Wright et al., 2002; Hikosaka 2005; Vincent, 2006). Conversely, fertilization has a positive effect on growth and induces a decrease in LL associated with an increase in RR PPL (Balster and Marshall, 2000; Cordell et al., 2001; Amponsah et al., 2005; Ren et al., 2011). Thus, an increase of growth rate is accompanied by an increase in RR PPL and a decrease in LL. For example, species of the genus *Picea* characterized by a high growth rate exhibit higher photosynthesis rates and lower LL values (Kayama et al., 2007).

A positive correlation between the rates of growth and photosynthesis has been reported (Mokronosov, 1981). Pessimal environmental conditions have a negative effect on the rate of growth and P_a, and therefore the periods of leaf "maturation" (LL_g) and senescence (LL_s), as well as the entire LL, are prolonged. A decrease of the demand of growth zones (sinks) for photosynthesis products is accompanied by a decrease of P_a in situ, with a consequent decrease of RR PPL and increase of the LL. On the contrary, an increase in growth rate and P_a under environmental conditions favoring growth and photosynthesis is accompanied by an increase in RR PPL and a decrease in LL. This concept provides a satisfactory explanation for wide LL variability within a species, as well as that within an individual plant, if illumination is considered an environmental factor in the latter case. The considerable LL variability within an individual (Lizaso et al., 2003) can be due to changes of the positions of individual leaves relatively to the light source during plant growth and development. The degree of illumination of the leaf affects P_a, RR PPL, and LL.

Changes in chloroplast number and size are among the reasons of photosynthesis rate variability in plant species (Mokronosov, 1978). Analysis of the effects of illumination on these features of the leaf showed that a decrease in illumination was accompanied by a decrease in the number of chloroplasts, whereas the size of chloroplasts increased such that the cytosol volume occupied by all chloroplasts remained virtually constant (Tsel'niker 1978; Tsel'niker and Mai, 1979). The functional variability in chloroplast size is reportedly due to the accumulation of assimilated starch (Kursanov, 1976). The amount of starch per unit volume of the chloroplast stroma does not depend on the size and number of chloroplasts in the cell (Crumpton-Taylor et al., 2012), which provides indirect evidence of the virtual constancy of the cytosol volume occupied by chloroplasts in the mesophyll cells of a leaf of a certain species. The identity of the volumes occupied by all chloroplasts in the mesophyll cell of leaves of an individual species is probably due to the identity of PPL, which is genetically determined. For instance, the LL of light-exposed leaves is shorter, but the P_a is higher than in leaves of the same tree located in a shadowed area (Hikosaka, 2005; Kitajima et al., 2005; Lusk et al., 2010); therefore, the photosynthetic potential is almost identical for leaves of both types, although it is realized at different rates. A negative correlation between the chloroplast number in the cell and the average size of a chloroplast is not limited to intraindividual or intraspecies variability, since it is also observed upon interspecies comparisons: for instance, the chloroplast size is smaller in heliophytes than in scyophytes, while the number of chloroplasts per unit area of the leaf is higher in the former (Mokronosov, 1978). Therefore, PPL values for these species can be quite close. However, RR PPL is higher and LL is lower in heliophytes than in scyophytes, as was already mentioned above.

Genotypic features, which allow realization of the photosynthetic potential of a species over a short time, provide an advantage in competition with other species occurring in habitats favorable for growth and photosynthesis. Species of the type described above are characteristic of early stages of succession (Navas et al., 2003; Matsuki and Koike, 2006). Ruderal species exhibiting a high growth rate under favorable environmental conditions can be attributed to this type (Grime, 1979). Abundant fruiting of monocarpic ruderal species requires considerable amounts of photosynthesis products and fast realization of PPL associated with a decrease in LL, which can be interpreted as an increase in the aging rate of the leaf. On the other hand, genotypic features enabling the maintenance of a low RR PPL by the species for a long time provide an advantage in competition with other species inhabiting areas characterized by pessimal conditions for growth and photosynthesis. Evergreens can be named as an example of species of this type. They predominate in unproductive habitats with a poor soil and a deficit of light and water (Aerts 1995; Markesteijn et al., 2011). Such species are characteristic of late stages of succession (Navas et al., 2003; Matsuki and Koike, 2006). Stress tolerant species with a low growth rate (Grime, 1979) can be regarded as a species with a low RR PPL and a prolonged LL. Most succulents characterized by a long LL can be considered stress tolerant species (Terashima et al., 2001). A low growth rate and CAM type of photosynthesis, which involves nocturnal gas exchange with the environment, are characteristic of these plants. Part of the typical photosynthesis processes occurs in the daytime, when the stomata are closed, and therefore a specific approach not identical to that presented above is required to assess PPL in succulents. RR PPL can be assumed to be low, while LL or the longevity of chloroplast-containing photosynthetically active tissues can be assumed to be high in succulents with a low growth rate.

A decrease in the photosynthesis rate is a typical indicator of leaf aging (Buchanan-Wollaston, 1997; Guo and Gun, 2005). A decrease in RuBisCO synthesis not related to the nitrogen supply to the leaf is among the reasons for this decrease (Imai et al., 2008). The decrease of P_a in leaf ontogenesis starts almost immediately after leaf "maturation" (the attainment of $P_{a\,\max}$), but the rate of this process, which is reflected by RR PPL, may vary (Table 1). The RR PPL value characterizes the aging rate of a leaf, with lower values corresponding to slower aging and higher LL. This is in accordance with the proposed effect of metabolic rate on LL due to the association between the metabolic rate and the processes of leaf aging (Lim et al., 2007).

CONCLUSIONS

The photosynthetic capacity of the leaf of a specific genotype represents the maximal possible amount of CO_2 assimilated during the lifetime of the leaf. The rate of realization of the photosynthetic potential determines the lifespan of the leaf. Realization of the photosynthetic potential is accelerated (reduced) in environments favoring (suppressing) plant growth and photosynthesis, while the lifespan of the leaf is reduced (increased). Environmental conditions that cause complete arrest of photosynthesis and plant growth result in the termination of photosynthetic potential realization and death of the leaves in species with leaves not adapted to such conditions. Species adapted to environmental conditions preventing photosynthesis and plant growth stop realizing the photosynthetic potential after the beginning of the unfavorable period, with the leaves of such species assuming a resting state. The decrease in photosynthetic potential implementation rate and the increase in leaf longevity in plant species are accompanied by an increase in the construction cost due to the increase of the mass of the leaf not occupied by the photosynthesis system (chloroplasts). Cell walls, which provide the mechanical strength of long-lived leaves, account for the major part of this mass increase. The positive correlation between leaf payback time and leaf lifespan stabilizes leaf payback. The relative stability of leaf payback is due to the common reaction of chloroplasts of all species to the changes in the environmental parameters that affect photosynthesis. The environmental factors affecting photosynthesis determine the rate of photosynthetic potential realization and account for variability of leaf lifespan. Species with a short (long) leaf lifespan and a high (low) rate of photosynthetic potential realization are characteristic of early (late) succession. Species with a high rate of photosynthetic potential realization and a short leaf lifespan have competitive advantage under conditions favoring photosynthesis and growth, since they can use environmental resources for rapid growth and expansion. This group includes ruderal species. Species with a low rate of photosynthetic potential realization and a long leaf lifespan, such as stress-tolerant plants, are highly competitive under pessimal environmental conditions. A decrease in the photosynthesis rate is a typical sign of leaf aging. Rates of photosynthetic potential realization and leaf aging are low in evergreen species. There are two main reasons for leaf lifespan variability in higher plants: first, the characteristic features of the species not related to photosynthesis, and, second, the group of intrinsic and extrinsic factors that determine the photosynthesis rate in a given leaf.

ABBREVIATIONS

LCC_a—leaf construction cost per unit area that corresponds to the amount of CO_2 assimilated in order to form a leaf with a given area (mol CO_2 m^{-2}); ($LCC_a = LCC_m LMA$).

LCC_m—leaf construction cost per unit dry mass (the amount of CO_2 assimilated in order to form 1 gram of dry weight of the leaf, assumed to be constant at 0.05 mol CO_2 g^{-1} dry weight).

LL—leaf longevity, total lifespan of the leaf (days) ($LL = LL_f + LL_n$).

LL_f—functional leaf longevity, part of leaf lifespan during which active photosynthesis occurs.

LL_n—nonfunctional leaf longevity, part of leaf lifespan during which photosynthesis does not occur.

LMA—leaf dry mass per unit area, the ratio of leaf dry weight to leaf area (g m^{-2}).

LP—leaf payback, the relative number of days of photosynthetic activity required to compensate for the photosynthetic costs of leaf formation (LP = (LP_t : LL_f) × 100%); LP corresponds to the ratio of construction costs to photosynthetic potential (LP = (LCC_a : PPL) × 100%).

LP_t—leaf payback time, the number of days of functioning at an average rate of photosynthesis required for assimilation of the amount of CO_2 equal to the construction cost LCC_a ($LP_t = 2LCC_a$: $P_{a\ \max}$).

P_a—rate of photosynthesis per unit leaf area at sating light exposure (mol CO_2 m^{-2} day^{-1}).

$P_{a\ \max}$—maximal photosynthesis rate at sating light exposure per unit leaf area, maximal rate of photosynthesis for the whole period of leaf ontogenesis at saturating illumination per unit leaf area (mol CO_2 m^{-2} day^{-1}).

P_m—rate of photosynthesis per unit leaf dry mass at sating light exposure (mol CO_2 g^{-1}).

$P_{m\ \max}$—maximal rate of photosynthesis per unit leaf dry mass at sating light exposure, maximal rate of photosynthesis for the whole period of leaf ontogenesis at saturating illumination per unit leaf dry weight (mol CO_2 g^{-1} day^{-1}).

PPL—photosynthetic potential of the leaf, that is, the amount of CO_2 fixed during the lifespan LL_f of the leaf (mol CO_2 m^{-2}) (PPL = $P_{a\ \max}/2LL_f$).

RR PPL—the rate of realization of the photosynthetic potential of the leaf; corresponds to change of photosynthesis rate (acceleration) during the active functioning period of the leaf (mol CO_2 m^{-2} day^{-2}) (RR PPL = 2 $P_{a\ \max}$: LL_f).

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