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Adaptability of Woody Plants in Aridic Conditions

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1. Introduction

Ecological conditions and sources such as water, temperature, solar radiation, and carbon dioxide concentration are factors that limit plant growth, development, and reproduction. Deviations from the optimal values of these factors can cause stress. Plants are subjected to multiple abiotic and biotic stresses that adversely influence plant survival and growth by inducing physiological dysfunctions (Kozlowski & Pallardy, 2002). On the other hand, plants use different strategies for survival that are important for their distribution throughout various regions. Plants differ widely in their ability to adjust to a changing environment and the associated stress (Itail et al., 2002), including the ability to cope with drought (Kozlowski & Pallardy 1997).

Water deficiency is the most significant stress factor for plant growth and reproduction. Drought is mostly associated with the dieback of trees within various regions and throughout the world (Mc Dowel et al., 2008). However, physiological mechanisms of woody plant survival have not yet been described. According to Passioura (2002a), all mechanisms that support physiological functions of plants under conditions of limited water availability are mechanisms of stress resistance. These mechanisms have developed over a long period of time as part of plant adaptability. According to Jones (1993), there are three mechanisms for plant drought resistance. The first mechanism consists of avoiding water deficit and involves the limitation of transpiration and maximisation of root uptake. The second mechanism involves the tolerance to water deficit (Passioura, 2002b; Gielen et al., 2008), and the third mechanism optimises the utilisation of water (Jones 2004).

Plant water stress is the result of a disproportionate balance between the amount of received and released water through various interactions with plant growth, development, and biomass production. The interactions are modified by genetic properties of the specimen and by the character and degree of plant adaptation. The amount of water that a plant can receive depends on the water supply in the soil and on eco-physiological characteristics of plant roots. The transport of water enables for a potential water gradient between the atmosphere and soil, and depends on the hydraulic resistance of the root and stem vascular system. Another component of the water regime of plants - release through transpiration - is a function of the physiological availability and mobility of the water. Plant regulation of the stomata opening and transpiration depend on the pressure potential and other influencing factors. Maintenance of a positive pressure potential is therefore conditional for the survival of plants under drought. The water regime of plants is therefore an ensemble of

the physical and physiological rules of the water transport within the soil-plant-atmosphere continuum.

2. Distribution of the wild pear *Pyrus pyraster* (L.) Burgsd. and service tree *Sorbus domestica* L. in Slovakia

The wild pear and service tree are members of the rare woody plants in Slovakia. The wild pear often grows in the scattered vegetation of the landscape, but also on the forest margins mainly in communities of oak stands. The service tree appears mostly in the rural landscape, and mainly in vineyards and fruit orchards. In many European countries, wild pear and service tree are often sought after by landscape designers and foresters, because both species have aesthetic influence in the landscape, a good growth rate, and provide valuable timber.

The vertical distribution of wild pear has been documented mainly at lower altitudes up to 400 m (Hofmann, 1993; Schmitt, 1998; Wilhelm, 1998). The highest location found was at an altitude of 754 m in bundesland Süd-Niedersachsen und Nordhessen (Schmitt, 1998).

In Slovakia, wild pear grows in the lowlands to sub-mountain areas, up to an approximate altitude of 950 m (Peniašteková, 1992), and in some cases up to an altitude of 1163 m (Blatný & Šťastný, 1959). A detailed study on the environmental conditions of stands where wild pear naturally occurs was conducted in 1994-1999 (Paganová, 2003). The basic data were obtained from 64 locations (Fig. 1).

Stands with wild pear were located mostly on grazing lands, meadows, and in the scattered woodlands. Wild pear populations were also found along a dry stream channel (locality 8) and in a thin forest (location 21). Wild pear often grows on the forest edge (locations 30, 34, 41, and 48), or on former grazing land that gradually changed to woodlands (location 42, 55, and 56).

The majority of stands with wild pear (80%) were found at altitudes up to 500 m. The lowest location in Slovakia was at an altitude of 100 m (12 Solnička), and the highest analysed stand was at an altitude of 800 m (19 Jezersko) (Paganová, 2003).

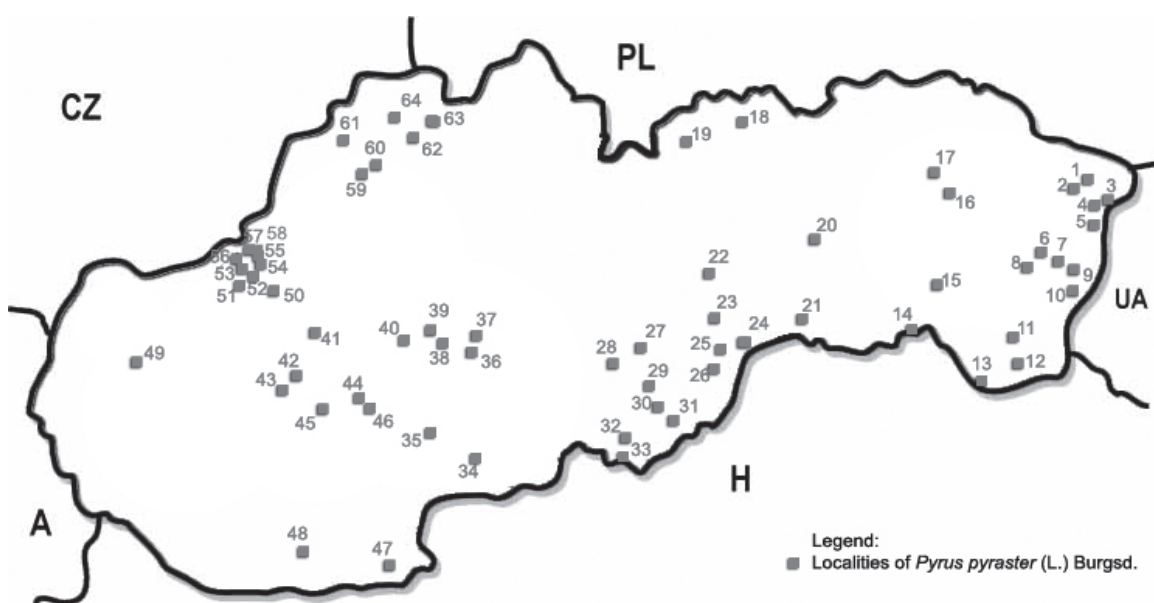


Fig. 1. Distribution of the wild pear (*Pyrus pyraster*) populations in the territory of Slovakia (Paganová, 2003).

The service tree is one of the rare autochthonous woody plants in the entire area of natural distribution. The area of natural distribution of the service tree reaches the northern part of Asia Minor and Africa as well as the northern border crosses of North Rhine-Westphalia, Lower Saxony, Saxony-Anhalt, and Thüringen, Bavaria. The northernmost occurrence is located in the Federal Republic of Germany at approximate latitude 51° of north width (Haeupeler & Schönfelder, 1988), and then continues to South Moravia and Slovakia, Hungary, Romania, and Crimea Mt.

According to Májovský (1992), the service tree has higher demands for light and high temperatures. In Slovakia, it is cultivated in the uplands on sunny south and southwest exposed stands. The vertical distribution of this woody plant occurs at an altitude of 109 m (Benčať, 1995) or 175 m (Michalko, 1961) up to an altitude of 610 m (Michalko, 1961; Benčať, 1995).

In 1996-2000, the environmental conditions of 24 locations of the service tree were analysed (Paganová, 2008). In Slovakia, the service tree appears in the southern regions in warmer stands at lower altitudes (Fig. 2). The distribution of the analysed stands containing the service tree confirmed its occurrence mainly at lower altitudes. The lowest stand with the service tree was found at an altitude of 200 m (location 23 - Vinné), and the highest stand was found at an altitude of 490 m (location 1 - Predpoloma) (Fig. 2).

The majority of the analysed stands containing the service tree (50%) were located in an open landscape near vineyards and fruit orchards (location 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, and 22). The service tree was frequently (46% of analysed stands) found in abandoned fruit orchards or on grazing lands as well (location 1, 2, 3, 4, 5, 6, 7, 19, and 20). Only a few plants were found in woodlands (location 23 and 24) and one stand of service tree (location 8) was located in an oak forest.

According to the analysis of the vertical distribution (Fig. 3), the service tree grows mainly on uplands in Slovakia. Approximately 66% of the analysed stands were found at an

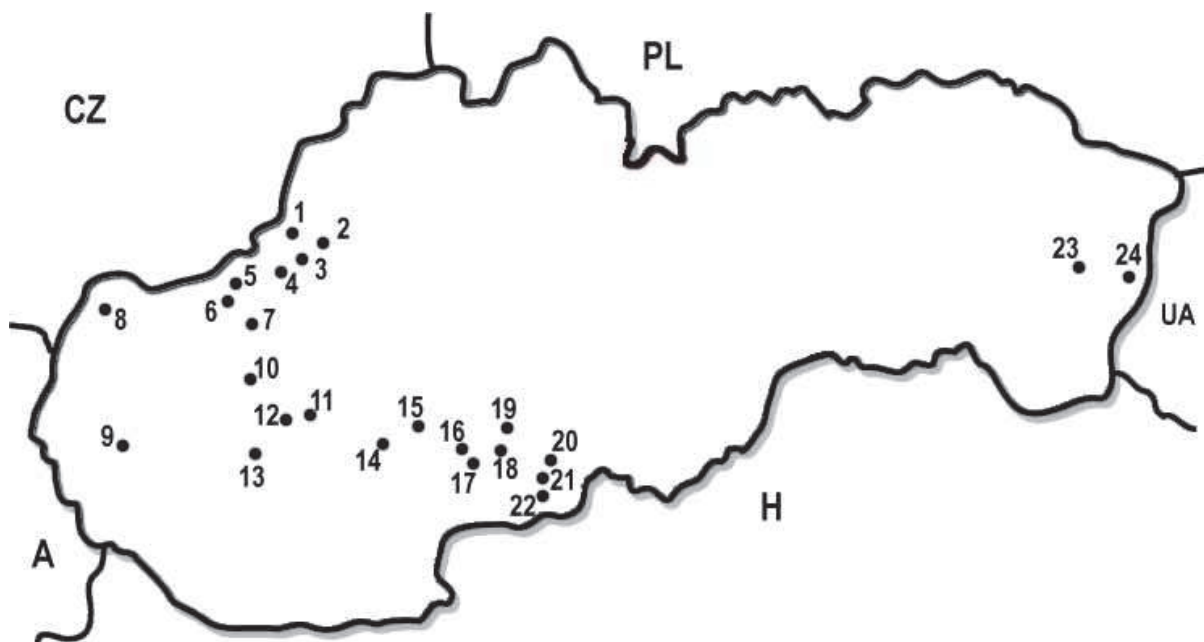


Fig. 2. Location of the stands with a higher number of service trees (*Sorbus domestica*) in Slovakia (Paganová, 2008).

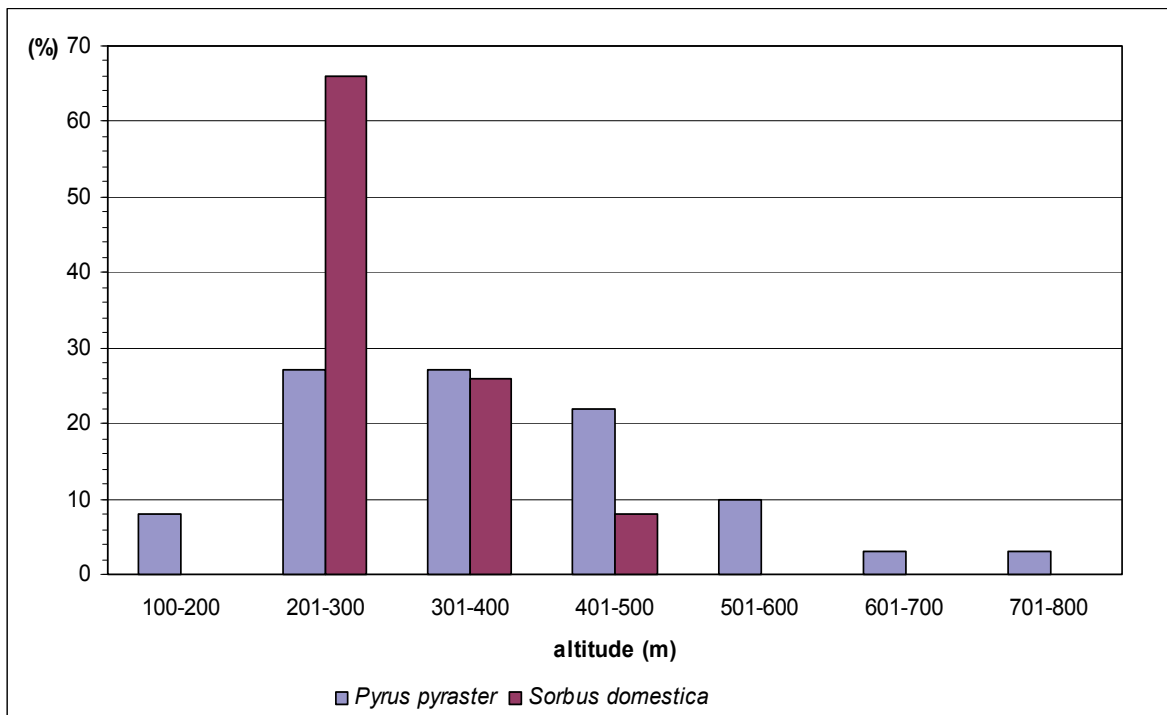


Fig. 3. Distribution of wild pear (*Pyrus pyraeaster*) and service tree (*Sorbus domestica*) in Slovakia according to stand altitude.

altitude of 201–300 m, and 26% of the stands were at an altitude of 301–400 m. One location was at altitudes of 450 m and 490 m. Compared to the wild pear (Fig. 3), the service tree is absent from the lowlands, and the occurrence of this woody plant at altitudes above 400 m is rare. According to Kárpáti (1960), the service tree is frequently found within communities of oak forests at lower altitudes and on fertile soils in communities of *Lithospermo-Quercetum*, *Melico (uniflorae)-Quercetum petraeae*, and others. Michalko (1961) confirmed the findings by Kárpáti, but according to his opinion, the service tree grows at higher altitudes only in extreme communities of *Corneto-Quercetum (pubescentis and petraeae)*, and can even be found in the beech woodland *Corneto-Fagetum* and in relict pinewoods growing on limestone and dolomite parent rock.

Similar to the data mentioned above, very similar findings regarding the range of altitudinal distribution were found in Switzerland. In this country, the service tree was found within an altitude of 384 m in the Basel region and 675 m in the Schaffhausen region (Brütsch & Rotach, 1993). In the southeast section of the Wiener Wald in the area of Merkenstein, the service tree has been found up to an altitude of 550 m (Steiner, 1995). At the northern border of its natural distribution in Germany in the region of Sachsen-Anhalt, the service tree is distributed from 140 m to 310 m, and predominantly within an altitude of 161–240 m (Steffens, 2000). On the Plateau of Lorraine, the service tree appears in forest crops at an altitude of 200–400 m (Wilhelm, 1998).

In southern regions of the natural distribution, the service tree grows at higher altitudes than in Slovakia. For example, in Spain, it grows at altitudes up to 1400 m, in Greece up to 1350 m, in Turkey up to 1300 m, and in southern Bulgaria from 300 to 800 m (Kausch, 2000). In southern Italy (Mt. Vesuvius), the service tree grows from the banks of the sea up to an altitude of 800 m (Bignami, 2000).

3. Ecological characteristics of the stands with *Pyrus pyraeaster* (L.) Burgsd. and *Sorbus domestica* L.

The wild pear is considered to be a light-demanding woody plant, which prefers warm stands with a sufficient amount of sunlight (Namvar & Spethman 1986; Hofmann, 1993; Wagner, 1995; Kleinschmit & Svolba 1998; Schmitt, 1998; Rittershoffer, 1998; Roloff, 1998; Wilhelm, 1998). Hofmann (1993) previously created a diagram for the occurrence of 300 wild pear plants according to the stand exposure. The plants were predominantly in locations with south and southwest exposures. In support of these findings, Roloff (1998) also found that the most frequent occurrence of wild pear plants was on slopes with a south or west exposure.

The service tree is explicitly regarded as a light-demanding woody plant (Michalko, 1961; Májovský, 1992; Brüttsch & Rotach, 1993; Pagan, 1996; Wilhelm, 1998). In Slovakia, 96% of stands with the service tree were found in the open landscape with solitary trees. Two stands were on the margin of woodlands with a few service trees in the crop, and only one location was an oak forest, with service trees found in the upper tree canopy or slightly above it. In all of these stands, the individual service trees grew under nearly full light without competition from other woody plants (Paganová, 2008). The service tree is intolerant to shading at an early age, and similar to the wild pear, will die quickly without a minimum light supply (Wilhelm, 1998).

Based on data obtained on the distribution of 507 wild pear plants in Slovakia, the majority of stands (80%) had a south, southeast, or southwest exposure. However, a limited number of stands (14%) containing wild pears were also found to have west, east, or northwest exposures, and four locations (6%) were on a plain stand (Fig. 4).

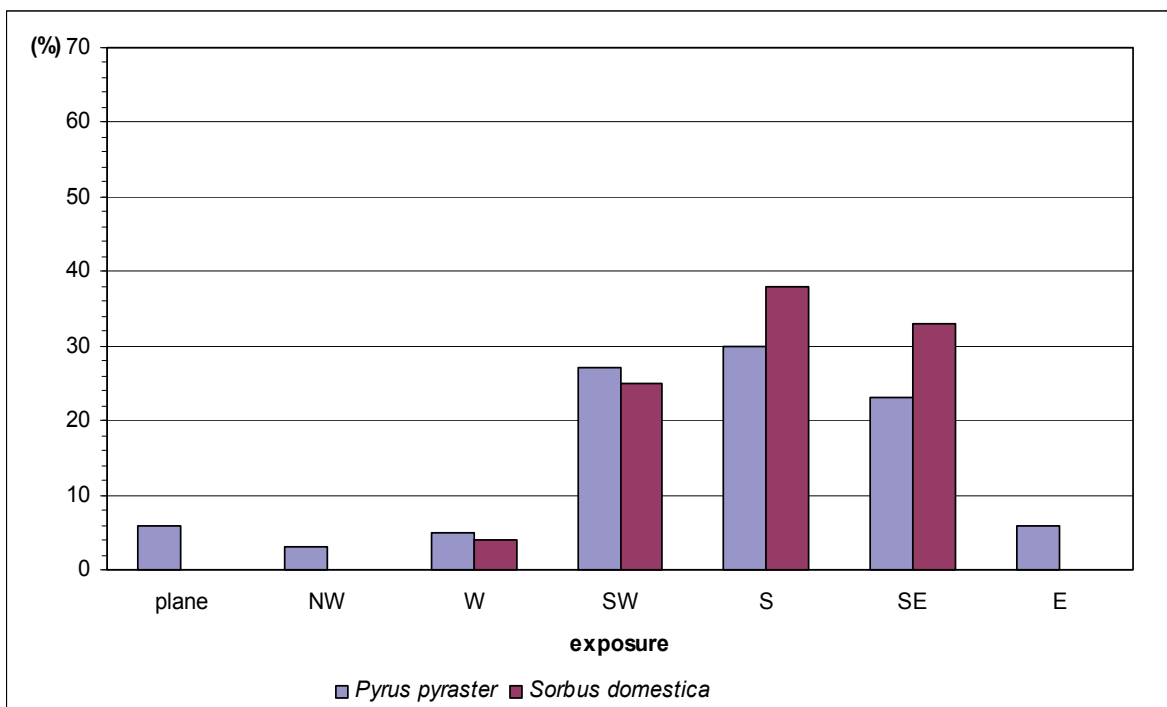


Fig. 4. The distribution of locations with wild pear (*Pyrus pyraeaster*) and service tree (*Sorbus domestica*) in Slovakia according to stand exposure.

In comparison to the wild pear, a majority of stands with service trees (38%) had a southern exposure, and many locations also had southeast (33%) and southwest (25%) exposures. One location (4%) had a western exposure. According to measurements by Geiger (1961), slopes with northern exposure obtain just half of the absolute total light emission as slopes with southern exposure. The prevalent distribution of service trees in southern-exposed stands supports the hypothesis regarding their high demand of light and warm climate. In Slovakia, none of the analysed locations had northern exposure. In Switzerland, 74% of the locations with service trees had southern exposure (Brütsch & Rotach, 1993).

The ecological-climatic amplitude of the wild pear locations in Slovakia is relatively wide. In stands with wild pear plants, the conditions range from plain and fold climates, to a mountain climate (Paganová, 2003). Stands were classified to climate-geographic types and subtypes according to Tarábek (1980) and Špánik et al. (1999).

Within the analysed scale of the wild pear stands in Slovakia, the average January temperatures range from -1.4°C to -5.8°C and the average July temperatures range from 13.5°C to 20.4°C . The annual sum of precipitation reaches values ranging from 570 mm to 900 mm. The majority of the pear locations (53%) fall within the climate-geographic type of mountain climate (Fig. 5), which is humid or very humid with rare temperature inversion. These stands were most frequently found in the warm and moderately warm subtypes of the mountain climate at an altitude of 250-550 m. The average January temperatures range from -1.4°C to -5.0°C , the average July temperatures range from 17.0°C to 20.4°C , and the annual sum of precipitation for these stands ranges from 580 mm to 790 mm.

Stands within the warm subtype of the fold climate are observed quite frequently. The fold climate is semi-humid to semi-arid with a remarkable inversion of temperatures. These locations are at altitudes of 210-450 m. The average January temperatures range from -2.0°C to -4.0°C , the average July temperatures range from 18.0°C to 19.2°C , and the annual sum of precipitation ranges from 628 mm to 765 mm in the respective locations.

The lowest number of wild pear locations was documented for stands in the warm or mostly warm subtypes of the plane climate, which is arid and semi-arid. Locations were registered at altitudes of 120-400 m. The average January temperatures in these stands range from -1.5°C to -3.3°C , and the average July temperatures range from 17.2°C to 20.1°C . The annual sum of precipitation is 570-700 mm.

The climate-geographic characteristics of stands with service trees are slightly different than stands containing wild pears (Fig. 5). The climate with the highest number of locations (42%) belongs to the mostly warm subtype of the plane climate, which is arid or semi-humid with a mild inversion of air temperatures. These stands are at an altitude of 200-300 m. The average annual temperature ranges from 8.3°C to 9.0°C , and the annual sum of precipitation is 610-650 mm.

A high number of stands (33%) were classified in the mountain climate with a mild inversion of air temperatures (the climate is rather humid). These stands are at an altitude of 220-490 m. The average annual temperature is 8.3°C and the annual sum of precipitation ranges from 650 to 620 mm.

The climate with the fewest locations of service trees was the fold climate (25%), which has a markedly high inversion of air temperatures (with an arid or even humid climate). The stand altitude ranges from 250 m to 380 m, the annual average temperature ranges between 8.1°C - 8.5°C , and the annual sum of precipitation is 620-700 mm.

According to a recent climatic evaluation (Škvarenina et al., 2004), the annual average temperature of the majority of locations with service trees is above 8°C , with the exception

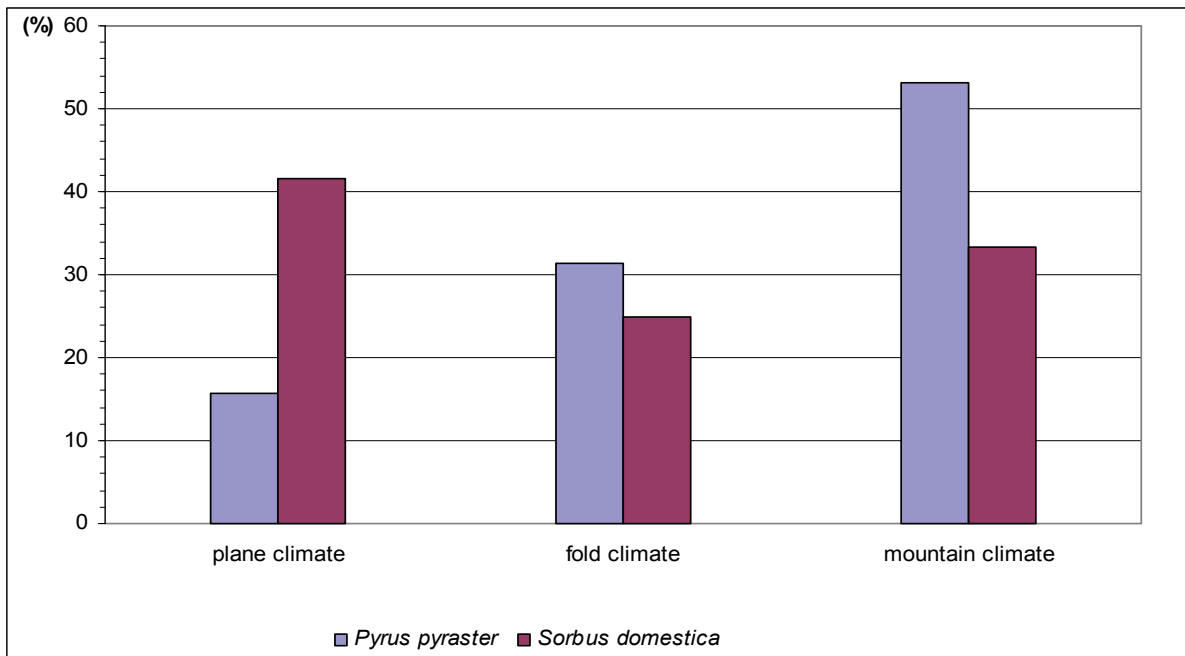


Fig. 5. Wild pear (*Pyrus pyraeaster*) and service tree (*Sorbus domestica*) stand classification in Slovakia according to climate-geographic types.

of two of the analysed locations (1 and 5), where the annual average temperature ranges from 7.5°C to 7.7°C. The average annual sum of precipitation for the majority of the stands is 610–700 mm, with the exception of the two mentioned locations, where this parameter reaches 790 mm and 750 mm, respectively. The potential evapotranspiration amount in the majority of the analysed stands was 600–750 mm during one year. Considering that the annual average sum of precipitation is 610–700 mm, it is possible that the service tree has to obtain enough moisture during the main growing season predominantly from water resources in soil. The deficit of rain during the summer occurs in the majority of the stands with this woody plant.

Warm and arid (southeast, south, southwest, and even west) stand exposures play an important role in the formation of the arid microclimate and mezzo-climate of the mentioned locations. According to climate classification in Slovakia (Špánik et al., 1999), the analysed locations with service trees were in warm and even moderately warm as well as semi-humid and even semi-arid climates. Compared to the wild pear, the service tree prefers stands at lower altitudes and is prevalent in warm and arid climates. The wild pear has wider ecological amplitude and grows at higher altitudes in stands with different water regimes and climate extremes.

Based on the brief pedology characteristics of our experimental plots, we can hypothesize that these soils are very well fertile (Chernozem, Fluvi-mollic soils, Cambisols, and Orthic Luvisols) or well supplied with nutrients (Luvisols, Pararendzinas, and Fluvisols). In addition, browned Rendzinas can be considered as relatively favourable soils.

According to the ecological scheme of Ellenberg (1978), the wild pear is a woody plant with broad ecological amplitude that grows in nearly all soil types, with the exception of extreme acidic soils. Rittershoffer (1998) found that mildly acidic or mildly alkaline soils were optimal for wild pear growth. According to information from Westfalen-Lippe (Germany), the wild pear prefers soils developed on limestone or on the rich nutrient

parent rocks (80% of stands) (Schmitt, 1998). In the area of Süd-Niedersachsen und Nordhessen (Germany), the wild pear frequently grows in shallow rendzinas from mussel limestone or from lime sandstone, and very rarely appears on deeper brown forest soils. More than 92% of all natural stands were on rich basic rocks (Hofmann, 1993). In the forest on the Plateau Lorraine, the wild pear grows mainly on parent rock of the mussel limestone and on keuper sediments. There are deep terra fusca soils and shallow Rendzinas (Wilhelm, 1998). The collective data from different areas of the natural distribution indicate that suitable growth conditions for the wild pear are mainly basic and rich nutrient soils with occasional water deficits.

In Slovakia, the wild pear grows on fertile soils (Chernozem, Fluvi-mollic soils, Cambisols, and Orthic Luvisols), or soils well supplied with nutrients (Albic Luvisol, Pararendzina, and Fluvisol). In addition, in some stands it grows on soils that are rich in minerals but under conditions of unbalanced soil chemistry with little fertility (Paganová, 2003).

In general, Fluvi-mollic and Cambisol soils have a sufficient water supply. At lower altitudes, the water deficit appears mainly in Rendzinas. The water deficit in Luvisols is usually a result of a lower amount of precipitation and higher evaporation. Orthic Luvisols have a lower water supply, and therefore the possibility of their aridization is higher. In addition, a fluctuating water regime appears within the Planosols and Fluvisols (Šály, 1988).

According to the ecological scheme by Ellenberg (1978), the wild pear has optimal growth conditions on fresh basic soils (its potential optimum). Another more frequent existence optimum of this woody plant is near the xeric forest limit, where the wild pear grows in arid soils rich in bases as well as in moderately acidic soils. Some authors have placed the wild pear among xerophytic woody plants according to its lower demands on soil humidity (Bouček, 1954). When under competition with some woody plants, it grows on its synecological optimum in extreme arid stands - rocky hilltops, stands of the xeric forest limit close to steppe communities, and in the sparse xerophytic oak woodlands (Rittershoffer, 1998). However, another existence optimum of this woody plant occurs in the hydric forest boundary in stands of the hardwood floodplain forests, where wild pear growth is limited by inundation (Rittershoffer, 1998). Based on these findings, the wild pear is a flexible woody plant with tolerance to a large range of soil humidity.

In Slovakia, stands with the service tree have favourable physical characteristics, good saturation, and are very fertile (Orthic-Luvisols and Cambisols), or have soils that are well supplied with nutrients (Rendzinas). However, under conditions of unbalanced soil chemistry, there is little fertility, and the pH of this soil is moderately acidic, neutral, or moderately alkaline. Cambisols generally have a sufficient water supply, and Orthic-Luvisols have a lower water supply with the possibility of aridization. Water deficiency can appear in Rendzinas as a result of the water penetration, so the water supply in this soil is usually low (Šály, 1988).

According to Wilhelm (1998), the service tree grows on mussel limestone and on keuper sediments on the Plateau Lorraine. These soils are well or very well supplied with nutrients. On slopes based with mussel limestones are deep terra fusca soils, and in the upper parts of the slopes are shallow Rendzinas. On the keuper, there are abundant, deep Vertic Cambisols with water deficiency during summer.

In east Austria, the service tree grows in the oak forest communities and is considered to be a woody plant of the uplands with less demands on soil humidity, but with quite high demands on the nutrient content of the soils (Kirisits, 1992). In the Wiener Wald (Steiner, 1995), the service tree appears on limestone and dolomite parent rock with prevalence in

semi-humid and arid Rendzinas. In addition, the service trees in Switzerland are found mainly in arid soil with less skeleton that is rich in bases (Landolt, 1977; Brüttsch & Rotach, 1993), as determined from detailed studies of the service tree stands in Canton Genf, which refer to the medium deep and deep skeletal Cambisols and Luvisols with slower water penetration and possible water logging. In the Basel region, the service tree also grows on Rendzinas or Lithosols, which are shallow and extreme skeletal soils that have a very low water capacity. In the Schaffhausen, approximately 92% of the service tree plants grow on limestones, and the rest of the stands grow on gravels of the high terrace that belong to Riss. In the deeper strata, there are limestones that are part of the morena and gravels. Various soils, even acidic soils, can appear randomly on small areas of the parent rocks. These data document quite a broad range of soil conditions for the stands containing service trees, and tolerance of the taxon to periodic or rare occurrences of water deficit in the soils is evident. On some stands within the area of its natural distribution, the service tree grows under conditions of a soil drought.

4. Potential adaptability of the analysed woody plants to progressive drought

Drought can be considered in meteorological, agricultural, hydrological, and socio-economic terms (Wilhite & Glantz, 1985). Meteorological drought reflects one of the primary causes of drought. It is usually defined as precipitation less than a long-term average (defined as normal) over a specific period of time. Agricultural drought is expressed in terms of the moisture availability at a particular time during the growing season for a particular crop. Hydrological drought is usually expressed as a deficiency in surface and subsurface suppliers, and refers to a period when stream flows are unable to supply the established users under a given water management system. Socio-economic definitions of drought relate to the supply and demand of specific goods. Importantly, humans can create a drought situation through land-use choices or an excess demand for water (Wilhite & Glantz, 1985).

According to Škvarenina et al. (2009a), drought is a temporary aberration that differs from aridity, which is restricted to low rainfall regions and is a permanent feature of the climate. The altitude and topography are significant climate-differentiating factors. In Slovakia, a considerably broken topography plays an important role in the variability of climate conditions. The increase in altitude causes changes in solar radiation as well as thermal and water balance of the land (Škvarenina et al., 2009a). Vertical differentiation of the climate conditions has a significant influence on species structure of the natural vegetation. The biogenocenoses can be classified into nine vegetation stages described by Zlatník (1976) based on altitude, exposure, and topography, which are named after woody plants that are dominant in the area.

Škvarenina et al. (2009a) analysed trends in the occurrence of dry and wet periods in altitudinal vegetation stages in Slovakia between 1951 and 2005. The authors considered relative evapotranspiration (E/E_0), which is defined as the rate of the actual evapotranspiration (E) to potential evapotranspiration (E_0), as an excellent measure of water sufficiency for vegetation. According to their findings, the smallest annual values of (E/E_0) were recorded in the Danube lowland (1st Oak vegetation stage) with relatively high totals of potential evapotranspiration (E_0) above 700 mm and with annual precipitation totals below (P) 550 mm. The lowest value of the relative evapotranspiration (approximately 60%) was recorded in the lowest areas of Slovakia with an altitude up to 200 m. Relative

evapotranspiration reached higher values towards higher vegetation stages (above 90% in the 4th Beech vegetation stage at altitudes above 650 m).

In addition to relative evapotranspiration, the drought index (E_0/P) has also been used to describe the relationship between the energy and precipitation (P) inputs within particular vegetation stages. Warm forest-steppe stands in Slovakia with oak communities have drought index values (E_0/P) of approximately 1. The predominant areas of Slovak forests are stands with drought index values up to 0.3. Moreover, the vegetation stages with $E_0/P < 0.3$ are within the mountain climate (Škvarenina et al., 2009b).

In Slovakia, wild pear stands are distributed from lowlands up to an altitude of 800 m. Specimens also appear in 1st (oak) and 2nd (beech-oak) vegetation stages with a water deficit during the growing season. The stands in these vegetation stages are classified as a territory with a dry (arid) climate according to the relative evapotranspiration and drought index. On the other hand, the wild pear is also distributed in stands at higher altitudes in the 4th (beech) and 5th (fir-beech) vegetation stages, which have a higher humidity (higher relative evapotranspiration). This type of distribution shows that the wild pear is tolerant to different conditions of water sufficiency.

The service tree is predominantly distributed in the 1st (oak), 2nd (beech oak), and 3rd (oak-beech) vegetation stages in Slovakia, avoids lowland stands, and appears mainly on slope terrain of the forest steppe stands. This taxon often grows in conditions of warm oak communities with an arid climate. At higher altitudes, the service tree most likely avoids the consequences of a strong beech competition. In the Slovak lowlands, the absence of the service tree is most likely due to the higher underground water level and the intensive agricultural utilization of the land.

According to Škvarenina et al. (2009a), a markedly severe drought between 1951 and 2005 was only identified in the Danube Lowland (1st Oak vegetation stage) and in the Záhorská lowland (2nd Beech-oak vegetation stage) of Slovakia. Considering the natural distribution of the wild pear and tolerance to a wider range of water supply, this woody plant has the potential to adapt to the decreasing humidity of the Danube Lowland. The service tree has similar qualities and the potential to grow in arid conditions; however, this taxon is mainly found on the slopes of forest-steppe stands.

According to a drought analysis of the Slovak territory conducted on the climatic data obtained from 1960-1990, agricultural regions become more sensitive to conditions of climate change upon drought occurrence (Šiška & Takáč, 2009). The authors used two indices for spatial evaluation of drought conditions in Slovakia: the climatic index of drought and the evapotranspiration deficit. The climatic index of drought (K) was applied for the entire growing season (GS10 period) and $K_{GS10} = \Delta E$, where E_0 is the potential evapotranspiration during GS10 and R is the rainfall during GS10. The evapotranspiration deficit ΔE during the growing season was calculated as $\Delta E_{GS10} = E_0 - E$, where E_0 is the potential evapotranspiration during the main growing season (GS10) and E is the actual evapotranspiration during the main growing season.

Two very dry and hot regions were classified in Slovakia, the Danubian and east Slovakian lowlands, which represent maize production areas with a water deficit that exceeds 250 mm during the growing season. These evapotranspiration deficit values will most likely be present in river valleys up to altitudes of 300 m as well (Šiška & Takáč, 2009).

The findings described here support the hypothesis that a higher frequency of drought occurs in agroclimatic regions of the Slovak Republic. In the future, it is important to elaborate on several concepts of the stabilization of agricultural production against water

deficit and soil aridity. With the exception of breeding programs that focus on developing new crop varieties that can tolerate the changed climatic conditions and development of integrated irrigation systems, there are also possibilities for landscape stabilization using non-forest woodlands. These types of woodlands should be established with woody plants that are tolerant to water deficit and that are adaptable to dynamic changes of water regimes. The taxa analysed here, including the wild pear and service tree, belong among the prospective woody plant species that are suitable for planting in regions potentially endangered by droughts.

The described research focused on an analysis of the physiological parameters of two woody plant species (wild pear and service tree) under conditions of a regulated water regime and water stress. The aims of the study were to verify the adaptive potential of both taxa to drought, and to obtain information on the mechanisms used by these woody plants under conditions of water deficit.

5. Interspecific differences of the selected physiological parameters of woody plants

Woody plants make different ecological adjustments to water deficit, and can modify their physiological functions and anatomical structures for adaptation. Adaptability is a rather complex quality, and the explicit function of a typical plant response to water deficit is very difficult to define. Therefore, we established experiments that regulated the water regime of juvenile (two-year old) wild pear and service tree plants under semi-controlled conditions.

The plants were planted in pots (content 2 L) with mixed peat substrate enriched with clay (content of clay 20 kg.m⁻³; pH 5.5-6.0; fertilizer 1.0 kg.m⁻³). The potted plants were placed under a polypropylene cover with 60% shading. The plants were regularly watered and maintained on 60% of the full substrate saturation for 28 days. In the phenological stage of shoot elongation (at the beginning of June), the plants of both taxa were divided in two variants according to a differentiated water regime. Variant "stress" was supplied with water at 40% of full substrate saturation and "control" at 60% of full substrate saturation. The model of the differentiated water regime was maintained for 126 days (to the end of September). Sampling was performed at 14 day periods for both conditions.

The size of the leaf area (A) and leaf water content (LWC) were measured, and a determination of fresh weight (F_w) and dry weight (D_w) was done gravimetrically. The size of leaf area (A) was calculated from leaf scans using ImageJ software (<http://rsbweb.nih.gov/ij/>). The LWC and specific leaf area (SLA) were calculated according to the methods described by Larcher (2003). For metabolic characteristics, the total chlorophyll and carotenoid content were determined according to the methods described by Šesták & Čatský (1966).

Data were analysed from three growing seasons in 2008-2010 for each taxon under two variations of water regimes (40% and 60% substrate saturation). The relationship between SLA and LWC of the plants under stress and control conditions as well as changes in the assimilatory pigments during water stress were also analysed. A statistical assessment of these parameters was conducted by regression analysis using the statistical software Statgraphics Centurion XV (StatPoint Technologies, USA). A $P < 0.05$ was considered statistically significant.

5.1 The influence of water stress on the production of leaf dry mass

The different reactions of the analysed taxa (wild pear and service tree) to water stress were confirmed by the dry mass (DM) measurements taken under controlled and stress experimental conditions (Table 1). Under control conditions, the increment of leaf dry mass of the wild pear was $14.67 \text{ mg p}^{-1} \text{ d}^{-1}$ and the increment of leaf dry mass of the service tree was $18.37 \text{ mg p}^{-1} \text{ d}^{-1}$. Under conditions of water deficit (stress), the increment of the leaf dry mass of wild pear plants was $12.78 \text{ mg p}^{-1} \text{ d}^{-1}$ and the increment of leaf dry mass for the service tree plants decreased to $3.04 \text{ mg p}^{-1} \text{ d}^{-1}$. The impact of water stress on the wild pear was less significant, and this plant is probably more tolerant to drought. Importantly, the relationship to photosynthesis economy depends on the leaf structure. The wild pear is a typical taxon of sunny and arid stands, and contains heterobaric leaves. Parenchyma (or sclerenchyma) cells without chloroplasts accompany the vascular system, and similar to ribs, lead to the top (adaxial) or bottom (abaxial) epidermis (Essau, 1977; Fahn, 1990; Terashima, 1992). The tips (ribs) of the vascular bundles divide leaf mesophyll hermetically into compartments that are reciprocally isolated against gas exchange. In the compartments, the intercellular space is relatively small with low chlorophyll content. The compartments are similar to "open windows", which transmit visible light into the internal layers of the mesophyll (Liakoura et al., 2009). Heterobaric leaf structures are also significant because they allow for easier transport of water to the epidermis due to increased hydraulic conductivity. One predominant factor that limits plant transpiration is leaf area. The reduction of leaf area during water deficit is typical for plants from arid stands. Several authors (Reich et al., 2003, Wright et al., 2004; Niclas & Cobb, 2008) have confirmed the narrow relationship between leaf structure and function. Our comparison of the leaf area ratio to dry weight of the leaves (SLA) of the analysed species confirmed the interspecific differences (Table 1). Wild pear leaves with higher values of SLA were thinner than leaves of the service tree under control conditions. The leaf water content per unit of dry weight in pear leaves was higher than service tree leaves. In experiments with fast growing woody plants, Dijkstra (1989) confirmed the thinner leaves of these species as well as the presence of larger vacuoles in the cells, which accumulate a larger amount of water per unit of dry mass. In our experiments with wild pear, the values of SLA decreased after 70 days under both conditions (stress and control), and the pear leaves became xeromorphous. There were no significant differences in SLA values of the pear leaves after 70 days under the differentiated water regime or due to water stress (Table 1).

The different functional qualities of the leaves can be effected by 1) changes in the leaf structure, and 2) different compositions of the leaf, including sclerenchyma elements and organic compounds (lignins and phenols), which increase leaf dry mass as described by Mooney & Gulmon (1982) and Lin & Harnly (2008).

Interspecific differences in the reaction to water deficit were not confirmed in the analysed taxa of this study. However, at the beginning of the experiments and after 70 days of cultivation, the values of LWC of the wild pear and service tree plants were different, and these values did not change under conditions of water stress (Table 1).

Based on our analysis of the relationship between SLA and LWC, both of the analysed taxa maintained higher LWC with increasing values of the specific leaf area, regardless of the level of substrate saturation (Fig. 6, 7, 8, and 9). In addition, a significant linear correlation was observed between SLA and LWC under control and stress conditions without interspecific differences.

Physiological characteristics	Taxon							
	<i>Pyrus pyraister</i>				<i>Sorbus domestica</i>			
	control		stress		Control		stress	
	0 day	70 day	0 day	70 day	0 day	70 day	0 day	70 day
Size of the leaf area A (mm ²)	23 312	34 570	23 312	32 578	59 499	78 713	59 499	51 210
Specific leaf area SLA (mm ² .mg ⁻¹)	19.13	15.14	19.13	15.80	16.57	16.71	16.57	16.06
Leaf dry weight DW ₁ (mg)	1 176	2 203	1 176	2 071	3 488	4 774	3 488	3 275
Leaf water content LWC (%)	66.3	57.0	66.3	57.6	45.4	52.2	45.4	51.5
Chlorophyll content (mg.mm ⁻²)	515.7 .10 ⁻⁶	679.2 .10 ⁻⁶	515.7 .10 ⁻⁶	779.7 .10 ⁻⁶	333.9 .10 ⁻⁶	470.5 .10 ⁻⁶	333.9 .10 ⁻⁶	452.0 .10 ⁻⁶
Carotenoid content (mg.mm ⁻²)	110.2 .10 ⁻⁶	138.4 .10 ⁻⁶	110.2 .10 ⁻⁶	147.4 .10 ⁻⁶	76.3 .10 ⁻⁶	105.4 .10 ⁻⁶	76.3 .10 ⁻⁶	101.6 .10 ⁻⁶

Table 1. Physiological characteristics of leaves taken from 2-year old potted plants of wild pear (*Pyrus pyraister*) and service tree (*Sorbus domestica*) grown in conditions of differentiated water regime - control (60% of the full substrate saturation) and stress (40% of the full substrate saturation) conditions.

Plot of Fitted Model for *Pyrus pyraister* with 40% saturation of the substrate
 $LWC = 41,5452 + 1,03154 * SLA$

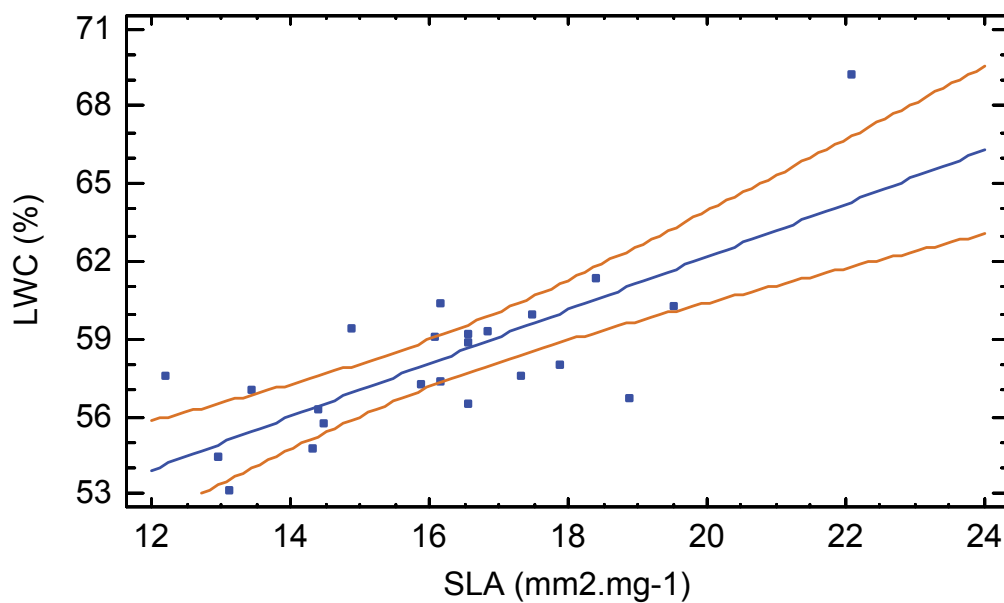


Fig. 6. Positive linear correlation between SLA (mm².mg⁻¹) and LWC (%) of wild pear (*Pyrus pyraister*) leaves under conditions of water stress. Correlation coefficient (r) = 0.760432, p value = 0.0000.

Plot of Fitted Model for *Pyrus pyraeaster* with 60% saturation of the substrate

$$\text{LWC} = 42,5661 + 1,06149 * \text{SLA}$$

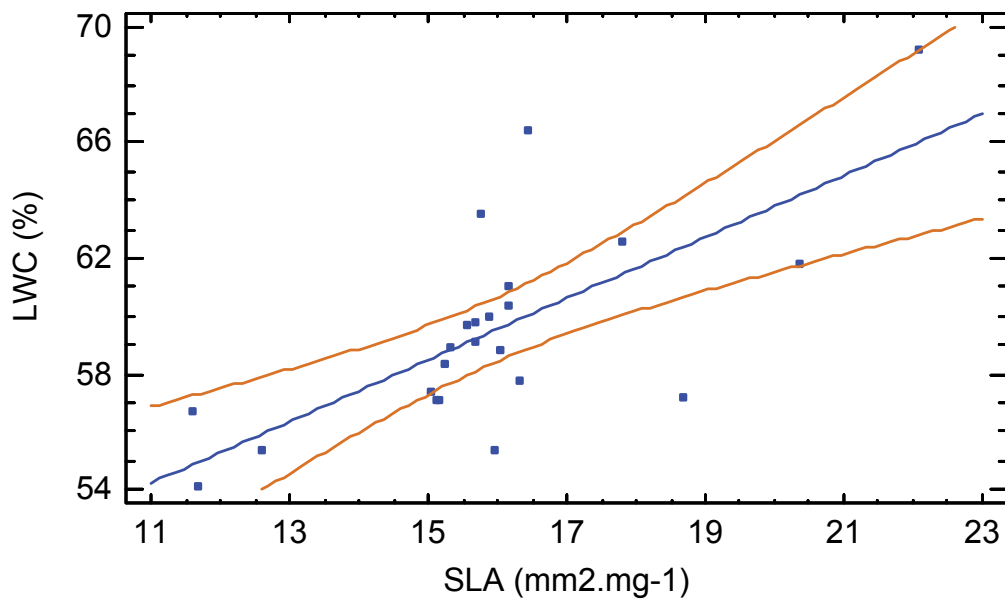


Fig. 7. Positive linear correlation between SLA ($\text{mm}^2.\text{mg}^{-1}$) and LWC (%) of wild pear (*Pyrus pyraeaster*) leaves under control conditions. Correlation coefficient (r) = 0.704177, p value = 0.0002.

Plot of Fitted Model for *Sorbus domestica* with 40% saturation of the substrate

$$\text{LWC} = 8,9215 + 2,46979 * \text{SLA}$$

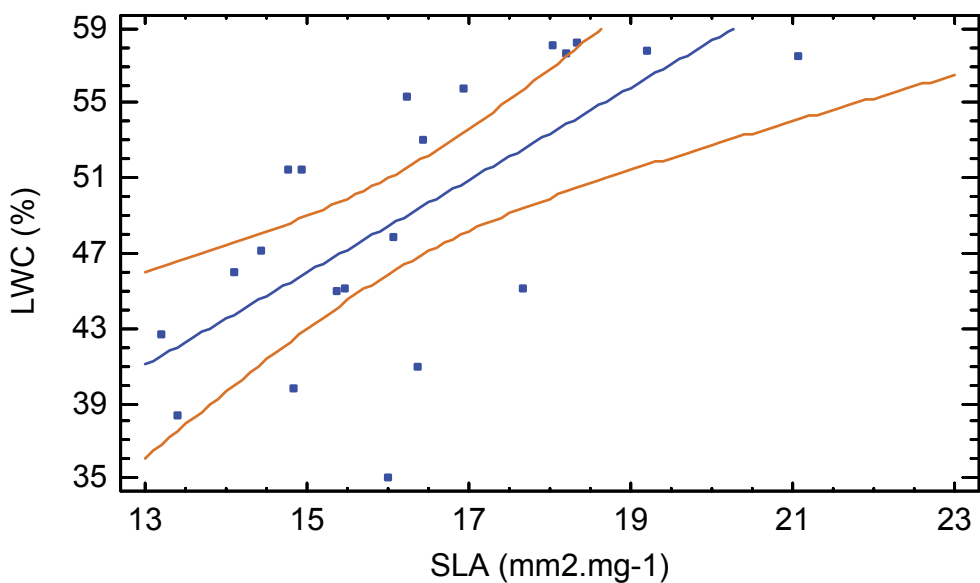


Fig. 8. Positive linear correlation between SLA ($\text{mm}^2.\text{mg}^{-1}$) and LWC (%) parameters of service tree (*Sorbus domestica*) leaves under water stress. Correlation coefficient (r) = 0.669898, p value = 0.0009.

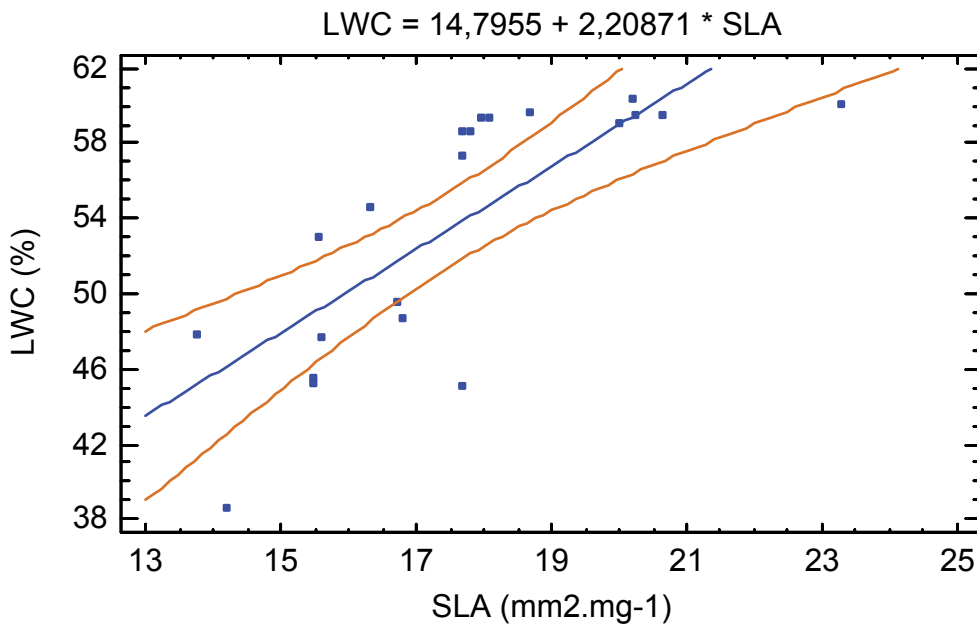
Plot of Fitted Model for *Sorbus domestica* with 60% saturation of the substrate

Fig. 9. Positive linear correlation between SLA (mm².mg⁻¹) and LWC (%) parameters of service tree (*Sorbus domestica*) leaves under control conditions. Correlation coefficient (r) = 0.76925, p value = 0.0000.

5.2 Changes in the assimilatory pigment content in leaves under conditions of water stress

The content of assimilatory pigments is an important factor that has a significant influence on thermal characteristics of the leaves. Leaves with lower chlorophyll content have higher reflexion, and the leaf surface temperature can have relatively lower values than the temperature of leaves with a higher content of assimilatory pigments. In addition, leaves with a higher content of carotenoids should have a relatively higher resistance against water stress. On the other hand, the ability of a plant to maintain a higher content of assimilatory pigments during stress can be very important for the functional activity of the leaves. Our analysis confirmed a different content profile of assimilatory pigments (chlorophyll a and chlorophyll b), β -carotene, and neoxantine in the leaves of the wild pear and service tree. There was a significant positive linear correlation between carotenoid and chlorophyll content in the leaves of both analysed taxa, regardless of the level of water saturation of the substrate (Table 2). This relationship is illustrated in Figure 10 for the wild pear plants at 40% substrate saturation. The results of the regression analysis for the wild pear under the control condition as well as for the service tree under both conditions are shown in Table 2. The SLA values of the service tree leaves did not change significantly under the differentiated water regime or under conditions of water stress (Table 1). The values of SLA in wild pear leaves decreased during the differentiated water regime under both conditions (control and stress). The decrease of SLA was most likely influenced by the specific quality of the taxon, which produces so called "summer leaves" during twig elongation. Two-year old plants of the service tree created leaves on terminal shoots only, and the values of SLA were not significantly changed in both variants of the water regime (control and stress) within the analysed period of time. During summer, the chlorophyll content in leaves of the wild pear increased under control and water stress conditions. The chlorophyll content in

taxon/substrate saturation	wild pear/40	wild pear/60	service tree/40	service tree/60
correlation coefficient r	0.973681	0.964724	0.982228	0.974045
p value	0.0002	0.0004	0.0005	0.0001

Table 2. Results of a simple regression between total chlorophyll content and carotenoid content in leaves of the analysed taxa wild pear (*Pyrus pyraster*) and service tree (*Sorbus domestica*) under two conditions of substrate saturation. Legend: 40 – conditions of water stress (40% substrate saturation); 60 – control conditions (60 % of substrate saturation).

Plot of Fitted Model for *Pyrus pyraster* with 40% saturation of the substrate

$$\text{CAR} = 47,0357 + 0,131496 * \text{CC}$$

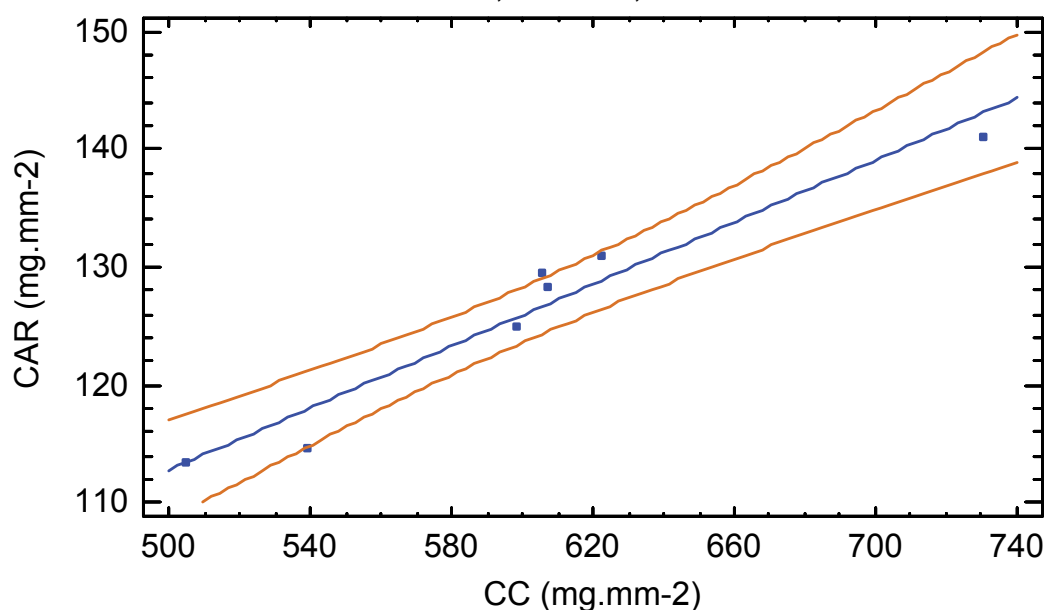


Fig. 10. Positive linear regression between total chlorophyll content (CC) and carotenoid content (CAR) in leaves of wild pear (*Pyrus pyraster*) plants growing under conditions of water stress. The correlation is quite close, with a correlation coefficient (r) = 0.973681 and statistically significant p value = 0.0002.

service tree leaves also increased; however, under water stress conditions, the chlorophyll content was lower than in the leaves of the control plants.

We confirmed a statistically significant relationship between SLA values and chlorophyll content in the leaves of the service tree under conditions of water stress, and this relationship was described by a polynomial curve of the second order (Figure 11). These data showed that the service tree maintained a balanced content of chlorophyll in leaves with a lower specific leaf area. In the stress variant, the chlorophyll concentration in service tree leaves varied between 340-470 $\text{mg}\cdot\text{mm}^{-2}$ within a 95% confidence level.

The relationship between SLA and chlorophyll content in the leaves of the wild pear under water stress conditions was also described as a polynomial function of the second order (Figure 12). However, this relationship was not significant. The leaf chlorophyll concentration ranged between 490-610 $\text{mg}\cdot\text{mm}^{-2}$ in the wild pear plants under conditions of lower substrate saturation (water stress).

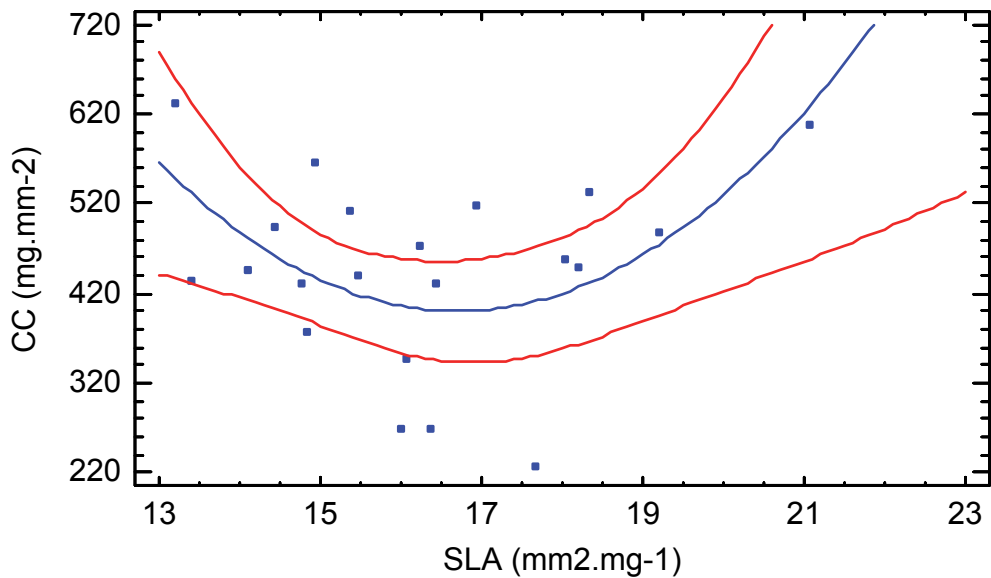
Plot of Fitted Model for *Sorbus domestica* with 40% saturation of the substrate

Fig. 11. Polynomial regression of the second order between specific leaf area (SLA) and chlorophyll content (CC) in the leaves of service tree (*Sorbus domestica*) plants grown under conditions of water stress. $R^2 = 30.92\%$; $p = 0.0358$.

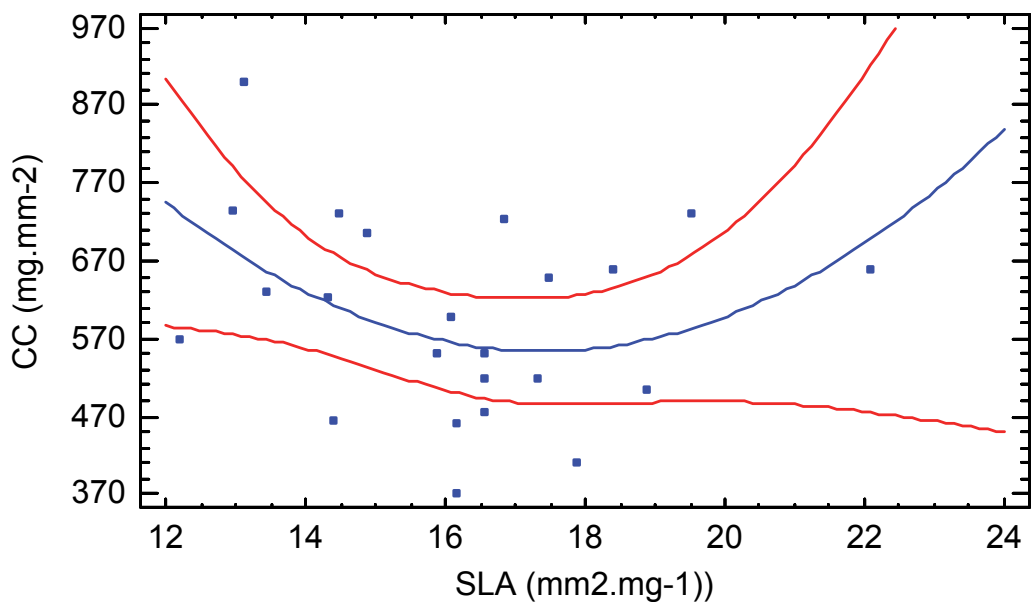
Plot of Fitted Model for *Pyrus pyraeaster* with 40% saturation of the substrate

Fig. 12. Polynomial regression of second order between specific leaf area (SLA) and chlorophyll content (CC) in the leaves of wild pear (*Pyrus pyraeaster*) plants growing under conditions of water stress. $R^2 = 18.3086\%$; $p = 0.1324$

According to the results obtained from experiments with the differentiated water regime, we found a non-significant influence of low substrate saturation on the metabolic processes related to chlorophyll production in both of the analysed woody plant species.

6. Conclusion

With regard to progressive aridization, the research of resistant autochthonous woody plants that survive in extreme drought conditions is considerable. We have studied two taxa that naturally grow in the cultural landscape of Slovakia – the wild pear and service tree. Both species are light-demanding woody plants and occur in similar stands. Compared to the wild pear, the service tree prefers stands at lower altitudes, and is prevalent in warm and arid climates. The wild pear has wider ecological amplitude, and also grows at higher altitudes in stands with a different water regime and climate extremes.

Two-year old plants of the studied taxa were used in experiments with a regulated water regime. The plant material was grown from seeds collected directly from original stands in Slovakia, and the plants were maintained under semi-controlled conditions with 60% and 40% substrate saturation. Under these conditions, we analysed the following parameters: leaf dry mass, size of leaf area, leaf water content, specific leaf area, and the complex of assimilatory pigments.

Assessment of the analysed parameters confirmed interspecific differences in the physiological reactions of the woody plants under regulated conditions of a water regime. Each of the studied taxa utilized unique drought tolerance strategies. Under a differentiated water regime, the wild pear produced and increased leaf dry mass regardless of the level of substrate saturation (water regime). Based on these findings, the wild pear uses this mechanism to resist drought conditions.

Interspecific differences between the wild pear and service tree were confirmed by measuring the specific leaf area (SLA) and leaf water content (LWC). Compared to the service tree, the wild pear had higher SLA values when provided with a sufficient water supply. The SLA values of both taxa had a positive linear correlation with the leaf water content (LWC). Under water stress conditions, the wild pear reduced SLA, which was influenced not only by water deficit, but also by different morphogenesis of the assimilation apparatus. During the experiment with the regulated water regime, the service tree had lower values of SLA than the wild pear and maintained them without significant changes, even under conditions of water stress.

A statistically significant relationship was confirmed between SLA values and chlorophyll concentration in the leaves of the service tree under conditions of water stress. This relationship was described as a polynomial curve of the second order. The relationship between SLA and chlorophyll concentration in the leaves of the wild pear under water stress conditions was also described as a polynomial function of the second order; however, this relationship was not significant. The low level of substrate saturation did not significantly influence metabolic processes related to chlorophyll production in both of the analysed taxa. The water regime of the analysed woody plants is the decisive factor that affects their distribution and survival in conditions of progressive aridization. Considering the natural distribution of these woody plants and their tolerance to a wide range of water supply, the wild pear exhibits good adaptability to decreasing humidity. The service tree has similar qualities and the potential to adapt to arid conditions; however, it is generally found on slopes of forest-steppe stands.

In the future, studies will focus on strategies of water utilization used by xerothermic woody plants under conditions of aridization. The photosynthetic activity and transpiration of woody plants will also be analysed under conditions of limited water supply. The research will focus on the photosynthesis, transpiration, stomatal resistance, structural leaf elements, and root system of woody plants.

7. Acknowledgment

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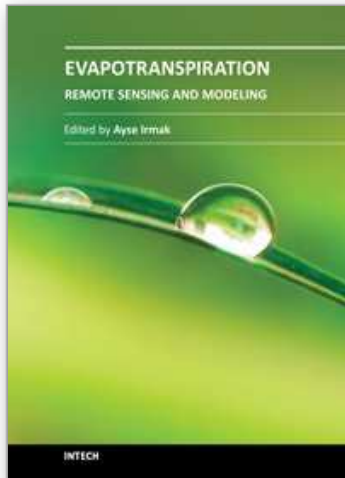
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This edition of Evapotranspiration - Remote Sensing and Modeling contains 23 chapters related to the modeling and simulation of evapotranspiration (ET) and remote sensing-based energy balance determination of ET. These areas are at the forefront of technologies that quantify the highly spatial ET from the Earth's surface. The topics describe mechanics of ET simulation from partially vegetated surfaces and stomatal conductance behavior of natural and agricultural ecosystems. Estimation methods that use weather based methods, soil water balance, the Complementary Relationship, the Hargreaves and other temperature-radiation based methods, and Fuzzy-Probabilistic calculations are described. A critical review describes methods used in hydrological models. Applications describe ET patterns in alpine catchments, under water shortage, for irrigated systems, under climate change, and for grasslands and pastures. Remote sensing based approaches include Landsat and MODIS satellite-based energy balance, and the common process models SEBAL, METRIC and S-SEBS. Recommended guidelines for applying operational satellite-based energy balance models and for overcoming common challenges are made.

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