

The Impact of Environmental Factors on Traits of Hedera Helix L. Vegetative Shoots

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Abstract

Hedera helix L. is an evergreen vine native to Europe. Nowadays it is commonly recognised as an expansive species, posing danger to biodiversity of natural ecosystems. Obtaining the relationships between morphological variability, productive parameters of vegetative individuals and variations in environmental factors (on the example of the Kórnik Arboretum) is important for understanding the successful adaptation and dispersion of *H. helix*. Thus, the issue of our studies was to find the link between environmental factors and different traits of *H. helix*. We collected data on leaf length, leaf width, leaf petiole length, plant stem length, and the number of leaves per stem. We assessed values of ecological plasticity and correlation between the studied parameters. The results indicated the tolerance of ivy to wide variation in edaphic conditions. The limiting environmental factors for growth of the studied subpopulations were soil moisture and soil shade. We found large variability of leaf morphometric parameters and shoot length. Close correlation links were detected between leaf length/leaf width, leaf length/leaf petiole length, and leaf width/leaf petiole length. The length of the average leaf was a more variable parameter than the width of the leaf under different values of light intensity. Weak relationships were found between light intensity at the soil surface and plant stem length/the number of leaves per shoot. A high level of index of morphological integration of *H. helix* individuals and a close relationship between the quality index/subpopulation composition were established in this study. A direct relationship between light intensity and specific leaf area values was established. The value of specific leaf area decreased linearly with increasing of light intensity at the soil surface.

1. Introduction

Hedera helix L. (English ivy, common ivy, European ivy) belongs to the *Araliaceae* family (Wen et al. 2001; Ackerfield and Wen 2003; Metcalfe 2005). Ivy can be found in different life forms: perennial evergreen woody vine or climber, an herb, a woody subshrub, or rarely a tree (Putz 1984; Grime et al. 1998; Metcalfe 2005). Ivy is native to the Mediterranean and Atlantic regions (European species), while its northern and eastern limits in Europe run through southern Scandinavia, the Baltic countries, Belarus, Ukraine, and the Balkans. *H. helix* is now widely introduced into temperate parts of the world (Green et al. 2011), having become naturalized in Australia, Brazil, Canada, Hawaii, New Zealand, India, South Africa and the continental United States (Rose 1996; Laroque 1998; Swearingen and Diedrich 2000; Strelau et al. 2018). Ivy has spread to many natural areas and is increasingly becoming recognised as a danger to natural ecosystems (Clements and Ditommaso 2011; Strelau et al. 2018). Moreover, its invasion of woodlands and forests is associated with natural or anthropogenic disturbance, as well as forest plantations (Schnitzler and Heuzé 2006). It is particularly expansive in deciduous forests, where it can take advantage of the extra light in the winter (Okerman 2001).

The eastern part of Poland lies at the European eastern border of the *H. helix* range. The density of ivy's natural locations within the country decreases from west to east and northeast (Boratyńska 1987; Zajac and Zajac 2001; Koziarz 2015). European ivy is an ecotone species, occurring in fringe communities, in deciduous and mixed deciduous forests in fresh and moist habitats, occupied by oak-hornbeam and riparian alder-ash forests in Central Poland (Koziarz 2015). In Poland, the specimens of ivy were subjected to legal protection in 1946–2014 (Romuald 1979; Regulation of the Minister of the Environment 2014). Since the mid-20th century, the ivy, a species rarely reproducing generatively, has become an expansive plant with a growing number of sites where flowering and fruiting individuals are encountered (Kucharski et al. 2019). Owing to its clear range limits

(both altitudinal and northeastern) and structural features, ivy has long been considered a species particularly suited to monitoring the shift of forest types because of climate change (Walther 2002).

English ivy has distinctive juvenile and adult phenotypic characteristics (Bunk et al. 2019). The juvenile period is long, often lasting 15 years or more (Reichard and Hamilton 1997). Phenotypically, juvenile leaves are shade leaves and adult leaves are sun leaves. The most commonly recognised form of *H. helix* is the juvenile, with its palmately lobed leaves (3–5 lobes) that are dark green and glossy with whitish veins (Okerman 2001; Metcalfe 2005). The juvenile form cannot produce seeds, but it can reproduce vegetatively and it is typically this growth phase that produces adventitious roots (Okerman 2001). During the juvenile or non-reproductive stage, *H. helix* is typically a ground cover growing to a height of 50 cm (Metcalf 2005). The leaves of the adult or reproductive form are usually a lighter green, thick, ovate to rhombic in shape and have less prominent whitish veins. During the adult stage, *H. helix* produces terminal clusters of greenish-white flowers in the fall, which are pollinated by wasps, bees, and flies. The following spring *H. helix* produces a dark purple, fleshy drupe (fruit). Generative organs of the ivy appear on the shoots climbing the trunks of trees only when the diameter of the ivy shoot exceeds 1 cm at the height of 1.3 m above ground (Green et al. 2011). The natural switch in morphogenesis from juvenile to adult phase is a consequence of differential DNA replication. Reversal may also occur naturally in low light and high temperatures, and cuttings from the adult phase may revert to the juvenile phase (Ackerfield and Wen 2003; Rogler and Hackett 2006).

Ivy has a wide potential ecological niche under edaphic factors. It grows well in warm conditions in general, and is an indicator of warm conditions (Ellenberg 1998). Ivy is favoured by moist fertile or very fertile soils ranging from fairly dry to slightly damp; so it is common on heavier clay-rich soils and less abundant on poor and well-drained sandy soils (Thomas 1998; Metcalfe 2005).

The limiting environmental factors for ivy are moisture of soil and soil shade (Ellenberg 1998; Koziarz 2015). Ivy is semi-shade plant (Ellenberg 1988; Sack et al. 2003). Several studies (Hoflacher and Bauer 2006; Sack and Grubb 2002; Schnitzler and Heuze 2006; Stafne et al. 2005) indicate that English ivy grows in a wide range of light conditions, from full shade to full sunlight. Ivy seedling density was strongly positively correlated with soil moisture in shaded conditions (Kollmann and Grubb 1999). Shade plays a protective role, reducing evaporative demand and the impact of photoinhibitory irradiance (Sack and Grubb 2001; Sack 2004). Ivy has a relatively low light compensation point compared to other climbing plants (Carter and Teramura 1988). Vegetative leaves have lower photosynthetic capacity and have limited acclimation to high light fluxes (Bauer and Thöni 1988; Hoflacher and Bauer 2006). Adult leaves always have a greater photosynthetic capacity than juvenile leaves from the same plant (Bauer and Bauer 1980). Leaves show limited acclimation to moderately high light during leaf development, or even on exposure to higher light after full development (Bauer and Thöni 1988). Sun leaves which are exposed to a significant increase in ambient light in autumn show reduced net photosynthesis (Oberhuber and Bauer 1991). Ivy shows moderate morphological plasticity in shade with higher specific leaf areas (SLAs) when grown in deeper shade (Sack and Grubb 2002). Leaves absorb some energy by sharp increases in both reflectance and transmittance. Light quality has impacts on vitality and growth of *H. helix* (Sack and Grubb 2002). Although the above-mentioned studies deal with the ecological properties of vegetative ivy, there are no studies which examine the variation of leaf and shoot traits in different soil, light and moisture conditions. Therefore, the issue of the link between environmental factors and vegetative phase of growth of *H. helix* in connection with the expansion and its wide ecological amplitude is

relevant. Taking into account results of previous studies we hypothesized that: 1) limiting environmental factors for growth of vegetative subpopulations of ivy were moisture and soil shade, 2) soil shade has the biggest impact on variability and plasticity of morphometric leaf traits, 3) vitality of *H. helix* subpopulations is the best in semi-shaded conditions. The current study aimed to assess the morphological/vitality/productivity spectrums of the vegetative stage of *H. helix* in subpopulation loci depending on changes in environmental factors.

2. Materials And Methods

2.1 Study site

The research was conducted during July-August 2022 on the territory of the Kórnik Arboretum (Western Poland; 52.2448°N, 17.09698°E, 75 m a.s.l.; Fig. S1). The study was conducted at the same hours of the day from 10 a.m. to 12 p.m. Eleven experimental plots 50×50 m (EP) for phytocenotic characteristics in different environmental conditions and dominant soil types of the Arboretum were laid out (Table 1). We identified the species in the field, and all identifications were verified in the laboratory. Analysis was carried out at the level of loci (clusters) of subpopulations of *H. helix* (Table S1).

Table 1
Phytoindicative analysis of edaphic (soil) factors

№ EP	Type and class of soil	Parameter	Edaphic factor (numerical score)							
			HD	FH	RC	SL	CA	NT	AE	LC
1	brown forest, sand	X_{ave}	11.7	5.1	7.2	6.3	7.4	6.1	6.8	5.0
		X_{min}	11.1	4.8	6.9	5.8	6.5	5.9	6.1	4.8
		X_{max}	12.4	5.7	7.6	6.5	8.1	6.3	7.5	5.3
		SD	0.229	0.213	0.198	0.201	0.626	0.119	0.514	0.236
2	low moor peat, peal	X_{ave}	11.6	5.2	7.1	6.7	7.5	6.7	7.2	5.9
		X_{min}	11.4	5.0	6.4	6.1	7.0	6.5	6.3	5.4
		X_{max}	12.1	5.5	7.9	7.3	8.5	7.0	7.9	6.3
		SD	0.204	0.335	0.341	0.302	0.541	0.213	0.649	0.616
3	low moor peat, peal	X_{ave}	11.7	4.9	7.3	6.5	7.9	6.5	7.0	4.1
		X_{min}	11.5	4.5	6.9	6.2	7.5	5.9	6.5	3.5
		X_{max}	12.5	5.1	7.5	7.0	8.2	6.8	7.5	4.5
		SD	0.471	0.234	0.240	0.256	0.221	0.310	0.432	0.272
4	low moor peat, peal	X_{ave}	11.5	5.3	7.2	6.6	7.7	6.4	6.6	6.8
		X_{min}	11.3	5.0	6.3	6.0	6.5	5.9	5.9	5.5
		X_{max}	12.0	5.5	7.6	7.5	8.2	6.5	7.0	7.8
		SD	0.177	0.151	0.416	0.311	0.297	0.157	0.548	0.621
5	anthropogenic soil, loamy sand	X_{ave}	11.6	5.3	7.3	6.7	7.6	6.8	6.6	4.2
		X_{min}	11.5	4.5	7.0	6.0	6.8	6.4	6.0	3.7
		X_{max}	12.0	5.7	7.7	7.5	8.0	7.0	7.0	4.4
		SD	0.151	0.243	0.354	0.217	0.438	0.242	0.374	0.204
6	anthropogenic soil, very fine sand	X_{ave}	11.4	5.3	7.3	6.8	7.3	6.8	6.8	5.3
		X_{min}	11.0	5.0	6.6	6.2	6.6	6.4	6.2	4.8
		X_{max}	12.2	5.6	7.5	7.3	7.8	7.0	7.0	5.7
		SD	0.217	0.197	0.307	0.185	0.346	0.196	0.243	0.301
7	anthropogenic	X_{ave}	11.8	5.3	7.1	6.8	7.3	6.4	6.8	5.1

	soil, sand	$X_{\min}$	11.5	4.9	6.9	6.6	7.0	6.0	6.1	4.8
		$X_{\max}$	12.5	5.5	7.5	7.2	8.0	6.8	7.2	5.6
		SD	0.289	0.216	0.159	0.169	0.325	0.209	0.198	0.324
8	anthropogenic soil, clay loam	X_{ave}	11.5	5.2	7.4	6.7	7.7	6.6	6.9	5.2
		$X_{\min}$	11.1	5.0	7.0	6.2	7.2	6.2	6.1	4.9
		$X_{\max}$	12.5	5.4	7.7	7.4	8.0	7.0	7.3	5.4
		SD	0.397	0.119	0.180	0.436	0.230	0.222	0.126	0.147
9	gley-podzolic soil, sand	X_{ave}	11.5	5.3	7.5	6.9	7.4	6.5	6.9	5.1
		$X_{\min}$	11.0	4.8	6.8	6.4	7.0	6.2	6.2	4.6
		$X_{\max}$	12.5	5.5	7.8	7.4	7.6	6.8	7.5	5.4
		SD	0.410	0.172	0.291	0.243	0.180	0.196	0.336	0.233
10	erosional belt soil with accumulation process, very fine sand	X_{ave}	11.2	5.5	7.6	6.9	7.0	6.3	6.9	5.8
		$X_{\min}$	11.0	5.2	7.2	6.5	6.5	6.0	6.4	5.2
		$X_{\max}$	11.8	5.7	7.9	7.5	7.2	6.6	7.4	6.2
		SD	0.327	0.206	0.166	0.335	0.222	0.180	0.354	0.262
11	erosional belt soil with denudation process, silt	X_{ave}	11.4	5.3	7.6	6.9	7.2	6.1	6.8	5.3
		$X_{\min}$	11.0	5.1	7.0	6.4	6.8	6.0	6.4	4.9
		$X_{\max}$	12.0	5.6	7.9	7.5	7.4	6.4	7.2	5.7
		SD	0.299	0.160	0.394	0.298	0.190	0.141	0.277	0.145

An increase in the number of ivy individuals in the vegetative stage of growth was recorded in the Arboretum recently. Individuals of the initial stages of ontogeny, as well as individuals of immature and virginal stages of the generative phase were not found in the experimental plots at the time of the study. Studied loci of subpopulations of *H. helix* were incomplete. The dominance of individuals of the juvenile phase of the vine's age composition was established. *H. helix* was a subedificator of the herbaceous layer and formed fixed synusia on EPs. The studied subpopulations were not inferior in their position in the artificial phytocenoses (by projected coverage) regardless of the inferiority spectrum of the ontogenic development. The horizontal composition of subpopulations was accidental. Vegetative reproduction was recorded.

2.2 Data analysis

2.2.1 Phytoindicative analysis. The phytoindication method was used to determine the rates of the main ecological factors (Didukh 2012). The parameters of edaphic factors were determined using unified scales of

environmental amplitudes. The effects of edaphic factors were analyzed: Hd – soil moisture, fH – variability of soil moisture, Rc – soil acidity, Tr – soil salinity, SI – general salt regime, Nt – available soil nitrogen, Ae – soil aeration, Lc – soil shade (light at the soil surface). The average score of the environmental gradient was determined for all species on EPs, taking into account the projected coverage of species. Six subplots 5×5 m (25 m²) were arranged within each EP (1–11) for the collects the geobotanic data.

2.2.2 Vitality composition and morphometric parameters. We measured only a representative subset of vegetative individuals. Seedlings were excluded from our study. The density and vitality composition for the analysis of the state of the subpopulations was established. Subpopulation density was calculated on 1 m² plots (four-fold replication on EP). A sample size of 20–25 vegetative individuals was selected from each subpopulation. The harvested ivy was separated into dry and green, and only the green stems were used for further biometric measurements in this study.

Vitality analysis was performed to assess the state of the individuals using a one-dimensional approach according to standard methods (Zlobin 2009). Vitality state of individuals of *H. helix* was determined by morphometric parameters: stem height (L_s), leaf petiole length (L_p), leaf length (L_l) and width (W_l), number of lobes per leaf (N_l) of average formation. Stem height was determined from soil surface to the tip of the top leaf with a measuring tape. Green leaves of each plant were counted. Morphometric measurements of leaves (L_p , L_l , W_l , N_l) in 20 replications for each shoot were carried out. Ecological plasticity of a leaf morphological parameter was calculated for each single plant as the difference between the maximal value and the minimal value of that parameter relative to the minimum of that parameter ($[max-min]/min$). The coefficient of variance was used to estimate the variability of the characteristics (CV, %). The following limits were established to identify the degree of variability of characteristics according to Pelabon et al. (2020).

The quality index of subpopulation places or sides or niches (Q) was determined as:

$$Q = 0,5 \times (a + b)$$

1

,

where a is the number of individuals in the first vitality class, and b is the number of individuals in the middle vitality class. The type is considered prosperous when $Q > c$, equilibrium when $Q \approx c$ and depressed when $Q < c$.

To assess the morphological integrity of plants, we used the morphological integrity index according to Zlobin (2009):

$$IMI = \frac{B}{(n^2 - n) / 2} \times 100, (2)$$

where IMI is the index of morphological integrity; B is the number of statistically significant correlation coefficients (p-value 0.95) in the matrix; n is the total number of estimated morphometric parameters.

2.2.3 Productivity parameters. Photosynthetic Active Radiation (PAR) was measured by Quantitherm PAR (Hansatech). Light intensity measurement was recorded at a height of 10 cm above climbing individuals of *H. helix* on each subplots (2.2.1). DLI (daily light integral) refers to the total amount of PAR expressed in units of moles per square meter per day ($\text{mol}\times\text{m}^{-2}\times\text{d}^{-1}$). Individuals of *H. helix* were divided into components (leaves, stem) and then dried in an oven with forced air circulation at 65°C to a constant mass. All components were weighed.

Specific leaf area (SLA) is a key trait with great ecological importance as it correlates with whole plant growth. SLA also responds to environmental changes. Specific leaf area (SLA) was calculated as:

$$SLA = \frac{LA}{W}$$

3

where LA is leaf area (cm^2); W is leaf dry weight (g).

LA was calculated by non-destructive method, based on the dimensions of the leaves (L_l , W_l) according to Rosu and Sala (2022):

$$LA = L_l \times W_l \times CF$$

4

where: L_l – leaf length (cm); W_l – leaf width (cm); CF – the specific correction factor for ivy leaves. The optimal value of the correction factor (CF) specific to ivy leaves was used according the proposed model by Sala et al. (2015).

2.2.4 Statistical analysis. Descriptive statistical analysis was used for the general analysis of the obtained field data and phytoindicative parameter values (min, max, average, standard deviation, standard error).

Interdependence relationships between morphological leaf parameters, ecological plasticity of measured traces, DLI were quantified by correlation analysis (Pearson), for which statistical certainty was also determined ($p < 0.05$; $p < 0.01$, $p < 0.001$). The variability within the data series was quantified for each morfometric parameter (coefficient of variation, CV). Linear regression analysis was used to describe the fit relationship between L_l , W_l and DLI, as well as other interdependence relationships between determined parameters, and for safety, p and R^2 parameters, and the F-test, were considered. Interdependence relationship between phytoindicative parameter values of edaphic factors, SLA, Q and DLI were considered by multivariate analysis (Principal Component Analysis). For the analysis and statistical processing of the experimental data, the mathematical calculation was used software OriginPro 2022.

3. Results

3.1 Phytoindicative analysis

Phytoindicative assessment of soil conditions on EPs was revealed by low/high ranges in the parameter values. Mesophytic conditions (by evaluation of Hd, fH) were predominant in the investigated area (Table 1). Water productivity of soil at the level of 100–145 mm was detected according to phytoindicative data. Index values of variability of soil moisture (fH) were 4.9–5.7. This marked the edaphic conditions, which were favorable for plants of fresh forest-meadow ecotopes with moderately uneven moisture of the root layer of the soil due to its complete wetting by precipitation and melt water (coefficient of unevenness of moisture $\omega = 0.17\text{--}0.23$ mm). The level of soil acidity (RC) on EPs was within the range of 7.1–7.9 (estimated as equivalent to pH 6.5–7.1), indicating that soil conditions were favorable for neutrophytes and sub-acidophilous plants. This was confirmed by the analysis of the species composition of the herbaceous layer on the EPs. Analysis of the salt regime (SL) ranged from 5.8 to 7.5. Such salt conditions were suitable for development of eutrophic plants, which grew on rich in salt soils ($150\text{--}200\text{ mg}\times\text{l}^{-1}$). The assessment of the nitrate soil regime was confirmed by dominance of nitrophilous plants on all EPs (soils with relatively high supplies of mineral nitrogen). The value of NT was ranged from 5.9 to 7.0. The higher values of NT were characteristic for EPs located on soils of anthropogenic origin. The evaluation of soil aeration (AE) showed that the conditions were suitable for growth of plants on dry loamy or wet sandy soils on all EPs. Species of this ecomorph had high occurrences on the EPs. The values of soil shade (Lc) had more variation in comparison with other environmental factors (3.5–7.8 score). The obtained values were confirmed by the species which dominated the herbaceous layers on the EPs. Soils of anthropogenic genesis were characterized by more variation in the numerical score of phytoindicative scales (Table 1). Principally, the obtained phytoindicative data on the Arboretum territory coincided with the main characteristics of the indicated soil types.

3.2 Morphological variability of diagnostic traces (parameters) of vegetative individuals of *H. helix*

Large ranges of the morphometric parameters of vegetative individuals of ivy were found. The width of the leaf of *H. helix* was varied from min 0.97 ± 0.43 cm (EP4) to max 12.34 ± 0.95 cm (EP1) among the studied EPs (Fig. 1a). At the same time, the average value of the leaf width varied from 3.31 to 6.39 cm. The maximum value of leaf length was recorded on EP3, EP6 and EP9. The average value of leaf length varied from 2.86 to 5.31 cm. The maximum values of length of the leaf petiole were recorded on EP1 and EP2, and the minimum values were found on EP10 and EP4. It should be noted that the average value of this parameter varied from 6.41 to 9.08 cm. The morphometric parameters with the highest variability among EPs were maximum length of the petiole and maximum leaf width. The most stable of the studied parameters of vegetative individuals of *H. helix* was leaf length.

Assessment of ecological plasticity of measured morphological leaf parameters showed different values. The ecological plasticity of the leaf petiole had the highest variability, corresponding to a high class of ecological plasticity, while the width and length of the leaf had an average value of ecological plasticity (Fig. 1b). The coefficient of variation for W_l ranged from 19.6% (EP9) to 36.3% (EP3), for L_l from 23.6% (EP4) to 29.1% (EP3), and for L_p 28.3% (EP7) to 42.3% (EP2). All investigated morphometric leaf parameters (according to the values of the variation coefficients) were assigned to the high class of variability.

The average length of juvenile shoots and the number of leaves located on them were also analyzed. The specified parameters had a wide range of variability among EPs. In particular, the maximum value of shoot

length occurred on EP2 (281.30 ± 14.07 cm) and the minimum value (130.38 ± 6.51 cm) on EP4. The coefficient of variation of shoot length was 14.7–31.1% (high class). The average length of the juvenile shoot was 213.15 ± 10.66 cm (SD = 42.40). The number of leaves on a juvenile shoot ranged from 28 (EP10) to 74 (EP2). The greatest number of leaves (74) was identified on juvenile shoots with the longest length on EP2. The minimum number of leaves was detected on a juvenile shoot with a length of 248.24 cm (EP10). The average number of leaves on a juvenile shoot of *H. helix* was 50 (SD = 15.61). The number of lobes per leaf of individual *H. helix* plants was 3–5 on all EPs.

A close correlation link was observed between the features of leaves: leaf length and leaf width (0.91), leaf length and leaf petiole length (0.87), leaf width and leaf petiole length (0.80). The weaker correlation link was detected between shoot height and leaf petiole length (0.76). The link between the number of leaves and their lobes was only 0.18. No more correlations were recorded between the specified quantitative traces at this level of reliability.

3.3 Subpopulation composition of *H. helix* as a function of vitality analysis

At the subpopulation level, most of the studied loci (according to the vitality analysis), belong to the prosperous type, while two loci were equilibrial (EP2 and EP10) and one locus had a depressive subpopulation type (EP 4) (Table 2). The highest values of the quality index (Q) had loci EP3 and EP6 subpopulations, and they were characterized by high abundance rates of individuals compared to other EPs of the Arboretum. It is worth mentioning that the share of c-class individuals was only 3% on EP3. Individuals of EP4 were characterized by the lowest values of the quality index (0.265) and the highest share of c-class individuals. IMI values range from 0.61 for locus on EP4 and up to 0.78 for the locus on EP3, indicating a generally high level of morphological integration of *H. helix* individuals.

Table 2
 Vitality composition of subpopulation loci of *H. helix*

No.EP	IMI	The share of plants by vitality classes			Quality index Q	Type
		a	b	c		
1	0.73	0.68	0.18	0.14	0.430	prosperous
2	0.65	0.44	0.23	0.33	0.335	equilibril
3	0.78	0.82	0.15	0.03	0.485	prosperous
4	0.61	0.29	0.24	0.47	0.265	depressive
5	0.72	0.70	0.19	0.11	0.445	prosperous
6	0.72	0.70	0.22	0.08	0.460	prosperous
7	0.70	0.64	0.23	0.23	0.435	prosperous
8	0.73	0.73	0.17	0.10	0.450	prosperous
9	0.70	0.67	0.24	0.09	0.455	prosperous
10	0.68	0.48	0.15	0.37	0.315	equilibril
11	0.73	0.66	0.19	0.15	0.405	prosperous

3.4 DLI, SLA and subpopulation composition

The conducted phytoindicative analysis indicated that the main limiting environmental factor of growth and dispersion of vegetative individuals of *H. helix* was soil shade. It was important to identify the dependences between light intensity and SLA. SLA is one of the objective components of the analysis of the environmental condition and plant growth, and it is mathematically scaled positively and linearly relative to the growth rate of the plant (Fig. 2). The values of DLI from $8.0 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$ to $13.0 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$ corresponded to the average values of SLA on EP1, EP6–EP9, and EP11. The values of SLA at the corresponding light intensity at the soil surface was from $182.04 \pm 9.13 \text{ cm}^2 \times \text{g}^{-1}$ to $186.02 \pm 9.34 \text{ cm}^2 \times \text{g}^{-1}$. The value of SLA decreased linearly to $109\text{--}112 \text{ cm}^2 \times \text{g}^{-1}$ with a further increase of DLI to $22 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$ and $25 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$, respectively. The maximum values of SLA were found on EP3 and EP5– $190.09 \pm 9.57 \text{ cm}^2 \times \text{g}^{-1}$ and $194.16 \pm 9.75 \text{ cm}^2 \times \text{g}^{-1}$ corresponding to the lowest values of DLI. The value of SLA was half as much ($84.03 \pm 4.26 \text{ cm}^2 \times \text{g}^{-1}$) at the maximum level of light intensity (DLI, $63 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$) on EP4.

The evaluation of the subpopulation composition showed that within the DLI range of $3\text{--}13 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$, the loci of *H. helix* retained a prosperous type (Fig. 2). The subpopulation locus changed to the depressive type on EP4 with increasing light intensity of soil. The equilibril type was characteristic of the average value of DLI. In general, the obtained data indicated that the reduction of SLA and the negative deviation of the vitality composition (from equilibril or prosperous condition) were associated with the stressful effect of the limiting factor of soil shade.

3.5 Link between morphological variability, SLA of *H. helix* and edaphic factors

The evaluation of phytoindicative score values of 8 edaphic factors/productive parameter SLA/vitality was carried out. The closest link between the value of SLA, the type of subpopulation (Q) and the phytoindicative value of soil moisture Hd (in one quadrant) was detected among the analyzed edaphic factors (Fig. 3). At the same time, inverse relationships were shown between SLA, Q and the Lc (opposite quadrants). The relationships between SLA, Q and Lc appeared to be closer (0.85 and 0.88) compared to Hd (0.76 and 0.77), respectively. The relationships between SLA, Q and other edaphic factors were not confirmed or were weak. The obtained results showed that the limiting edaphic factors which affected the vitality and dispersion of vegetative individuals of *H. helix* were to a greater degree soil shade, and to a lesser degree, moisture of soil.

The obtained data proved the necessity of analyzing the relationships between the variation of values of DLI and morphometric parameters. The difference of soil shade among the EPs of the Arboretum was closely related to the average values of the width and length of the leaves of vegetative individuals of *H. helix* (Fig. 4). A significant variability of the specified parameters was detected at DLI of $63 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$. Ranges in the variability of the specified parameters were insignificant at DLI up to $20\text{--}25 \text{ mol} \times \text{m}^{-2} \times \text{d}^{-1}$. We ascertained that the length of the average leaf was a more variable parameter than the width of the leaf under differences of soil shade. Analysis of the relationships between DLI and the average values of shoot length, leaf petioles, and the number of leaves per shoot of *H. helix* showed only weak relationships (Fig. 5).

In particular, the relationship between DLI and plant shoot length was the closest, but rather weak ($r=-0.58$). Weak relationships were detected between DLI and the length of leaf petioles/the number of leaves on the shoot ($r = 0.26$ and $r=-0.30$, respectively). The established relationship between the length of the shoot and the number of leaves was quite expected ($r = 0.75$).

4. Discussion

Hedera helix is often viewed as having a high potential impact on the environment and more specifically in completely covering the forest floor. This species is a versatile plant found in a variety of natural and human-induced habitats. A literature review indicated that English ivy seedlings establish on disturbed or open sites, although it may not establish well under frequent or severe disturbance (Metcalf 2005). Since the mid-20th century, *H. helix* with a weak capacity for generative reproduction, has become an expansive plant with increasing number of locations with flowering and fruiting individuals. It is worth mentioning that the juvenile phase typically forms the ground cover. The impulse for changes in the life strategy and dispersion of *H. helix* is the increase in the average air temperatures, precipitation and solar radiation intensity, which has been observed for the past several decades (Kucharski et al. 2019).

In Europe, at its northern, eastern and high altitude distribution limits, *H. helix* will remain at its juvenile phase (Andergassen and Bauer 2002). The increase in the number of individuals of *H. helix* in the vegetative stage of development and the formation of stable synusias on the Arboretum territory were confirmed by the existing data regarding the expansive characteristics of dispersion of this species in secondary or artificial parklands (Rackham 1990; Swearingen and Diedrich 2000; Kucharski et al. 2019). Juvenile leaves of the species formed

a thick canopy just above the ground and prevented sunlight from reaching other plants (Swearingen and Diedrich 2000). Other authors noted that foliage cover of individuals of English ivy grown in full sun was more than 20% (Stafne et al. 2005). The species with the most similar habitat preferences include *A. podagraria*, *B. ramosa*, *G. urbanum*, *F. vesca*, *M. uniflora* and *M. perennis* etc. (Grime et al. 1988; Metcalfe 2005) (Table S1). This study established that the listed species are typically interspersed with *H. helix* in the herbaceous cover.

H. helix appears to be tolerant of a rather broad spectrum of environmental conditions in the temperate zone. Ivy is classified as a moist-site indicator, being found mainly on soils of average dampness, and absent from both wet ground and places which may dry out (Ellenberg 1988; Kollmann and Grubb 1999). Ivy tolerates a wide range of moisture regimes (Reichard and Sarah 1996; Koziarz 2015). English ivy seedling density was positively correlated with soil moisture ($r^2=0.65$) and associated with relatively high soil moisture content (Kollmann and Grubb 1999). The phytoindicative study conducted here confirmed the results of other authors that the limiting environmental factors for the juvenile stage of growth of *H. helix* were soil moisture and soil shade. It has been shown that frequent short-term flooding has a positive effect on the growth of ivy, e.g. by increasing the availability of certain nutrients (Heuzé et al. 2009). *H. helix* is common on heavier clay-rich soils and less abundant on poor and well-drained sandy soils (Grime et al. 1988; Metcalfe 2005). Our data has proved the ecological dominance of the species in the fresh forest-meadow ecotypes of the Arboretum with moderately uneven moisture in the root layer of the soil. Researchers speculated that English ivy may be favored over other woodland species in Europe if climates become drier (Karl et al. 1995; Sack and Grubb 2002; Sack et al. 2003). A detailed understanding of the mechanism of water storage by ivy requires further research (Heuzé et al. 2009).

Ivy is tolerant of all but the most acid (< 4 pH), waterlogged or very dry soils. It is reported as growing well in acidic and basic soils (Reichard 2000) and tolerates a wide range of soil pH, but is most frequent and abundant above pH 6 and is seldom found below pH 4 (Grime et al. 1988). The results of this research indicated the tolerance of ivy for pH of 6.5–7.1.

Data on nitrate and total soil salinity as substrate conditions for *H. helix* are also shown in the literature. Ivy was often considered as a nitrogen indicator species which is also tolerant of salt deposition (Lameire et al. 2000; Binggeli 2005). Vidra et al. (2006) also found a positive correlation in an urban forest between exotic vine richness and soil fertility, with *H. helix* included as a vine. Our data provide additional information about this issue. In particular, it was found that *H. helix* grows on soils which are rich in salts and relatively high supplies of mineral nitrogen. The dense carpet of ivy often produced in some forests suppresses natural regeneration of understorey and forest species, possibly as a result of increased nitrogen levels produced by its leaf litter (Thomas 1998; Akerson and Gounaris, 2000; Reichard 2000). Nitrophile conditions of the edaphotope, with increase in phytoindicative point values up to 7.0. on Arboretum soils of anthropogenic origin, were obtained in this study.

The juvenile form of English ivy most often occurs in the shade (Hoflacher and Bauer, 2006; Metcalfe 2005; Schnitzler and Heuze 2006), while the adult form occurs in full sun (Miller 2003). Recently, mechanisms of the sun and shade leaf differentiation were reviewed (Terashima et al. 2005). English ivy's ability to adjust its photosynthetic capacity under variable light regimes may explain its tolerance to a wide range of light levels (Hoflacher and Bauer 2006). Adult leaves have a greater photosynthetic capacity than juvenile leaves, even on

the same plant (Hoflacher and Bauer 2006; Metcalfe 2005). Juvenile leaves, however, tolerated light and were not damaged by increased light. Both life phases of *H. helix* are capable of acclimating to strong light, but during the juvenile phase this capacity is not fully developed. However, several authors have claimed that juvenile leaves have only limited acclimation to high light fluxes (Hoflacher and Bauer 1982; Bauer and Thöni 1988; Hoflacher and Bauer 2006).

Juvenile individuals of *H. helix* were actively developed in the understory with low photosynthetically active radiation (PAR, $30 \mu\text{mol}\times\text{m}^{-1}\times\text{s}^{-1}$) and light intensity at the soil surface (DLI, $3 \text{ mol}\times\text{m}^{-2}\times\text{d}^{-1}$) (Carter and Teramura 1988). Our study confirmed the tolerance of vegetative individuals to changes in light intensity at the soil surface (DLI, $3\text{--}63 \text{ mol}\times\text{m}^{-2}\times\text{d}^{-1}$) without visible damage to the leaf surface. Acclimation behaviour suggests an ability to modify leaf structure at the level of tissue (Oberhuber and Bauer 1991). This opinion was confirmed by the morpho-histological characteristics of leaves of *H. helix* (water content and chlorophyll) at the different levels of light intensity (Baldini et al. 1997; Ganthaler et al. 2019). Ivy shows moderate morphological plasticity in shade, as expected of a shade-tolerator, with higher SLAs (Wright et al. 2001; Sack and Grubb 2002). Notably, SLA in high irradiance declined with increasing drought tolerance.

SLA ranged between $100\text{--}200 \text{ cm}^2\times\text{g}^{-1}$ in the shade/sun (Baldini et al. 1997; Sack et al. 2003). Ivy leaves show maximum absorbance between 400 and 700 nm, with a slight reduction in absorbance at around 550 nm (Baldini et al. 1997). Our study completely coincides with the data of other authors indicating a substantial alteration of SLA of juvenile *H. helix* leaves, depending on the light intensity at the soil surface.

We concur with the consequence that a significant fluctuation in SLA of *H. helix* is an ontogenetic strategy and a habitat-specific feature of resource allocation (Wyka et al. 2019).

How was the dual tolerance (moisture and light) of *H. helix* possible? Many traits can contribute to a reduced demand for irradiance and water simultaneously, such as small size (Grime 1966), long-lived leaves of low SLA (Cornelissen 1999; Wright et al. 2001), and a high below-ground allocation (Sack et al. 2003). Statistically positive correlation was found between soil moisture and SLA, too (Dogan et al. 2015).

In some locations, English ivy may reach its greatest abundance and vitality in shade. In particular, *H. helix* reached its highest frequency in a parklands on dark plots with less than 2.5% light transmission (Siebel and Bouwma 1998). Our study confirmed this phenomenon. The share of individuals of the highest development classes and, accordingly, the quality index of the subpopulation increased significantly at the lowest values of DLI. The type of subpopulation was deteriorated to the depressed type under conditions of intensive lighting (DLI more than $60 \text{ mol}\times\text{m}^{-2}\times\text{d}^{-1}$). English ivy had the greatest abundance and vitality in the shade. The relationship between the intensity of light at the soil surface and the vitality of *H. helix* was also given in other works (Sack and Grubb 2002). Some authors indicated a close relationship between the integrated variation in lighting/temperature and the fluctuation of stem length, SLA and other morphometric parameters (Pollet et al. 2009).

Morphometric parameters of leaves of vegetative individuals of *H. helix* are not only an indicative parameter that responds to modified environmental factors, but also a key feature for species identification (Ackerfield and Wen 2002). The authors recorded that the most indicative parameters of a leaf were number of lobes per leaf, length of the middle lobe, ratio of trichome center diameter to overall size, and overall width of the leaf.

The lengths of the leaf and the petiole of the leaf were revealed as indicative properties in this study. The maximum length of the leaf petiole for *H. helix* was previously set at 10.00 cm for the temperate zone of Europe. However, the maximum value of this parameter nevertheless reached 17.54 cm in our research. The weighted average, minimum and maximum values of width and length of leaf and number of lobes per leaf of *H. helix* were consistent with the reference data (Miller 2003).

Details on ecological plasticity of indicative leaf parameters of *H. helix* were recorded for the first time. It was confirmed that expansive species demonstrate significantly higher ecological plasticity than native plant species (Davidson et al. 2001). The identified ranges of the morphometric parameters of leaves of vegetative individuals due to diversity of light intensity coincided with the data of other authors (Baldini et al. 1997). Regardless, the link between variability of soil moisture and leaf morphometric parameters was not detected. This may be explained by the small amplitude of range of the humidity factor within the Arboretum.

Wide potential ecological niche, variability and ecological plasticity of morphometric parameters of leaves, and impacts of limiting environmental factors on the vitality of loci can explain the peculiarities of expansion and adaptation of juvenile individuals in artificial parkland. Determination of dependence between the variability of limiting edaphic factors of high amplitude of oscillation in different forest types and adaptive strategy of *H. helix* are future perspectives needed to clarify the reasons for the expansion of the species.

Conclusions

Wide potential ecological niche (phytoindicative analysis of edaphic soil factors), variability of morphometric parameters of diagnostic vegetative traces, ecological plasticity of morphometric parameters of leaves, impact of limiting environmental factor of soil shade on the deviation of the vitality composition (from equilibrial to prosperous condition) were detected at the level of loci of subpopulations of *H. helix*.

Declarations

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Figures

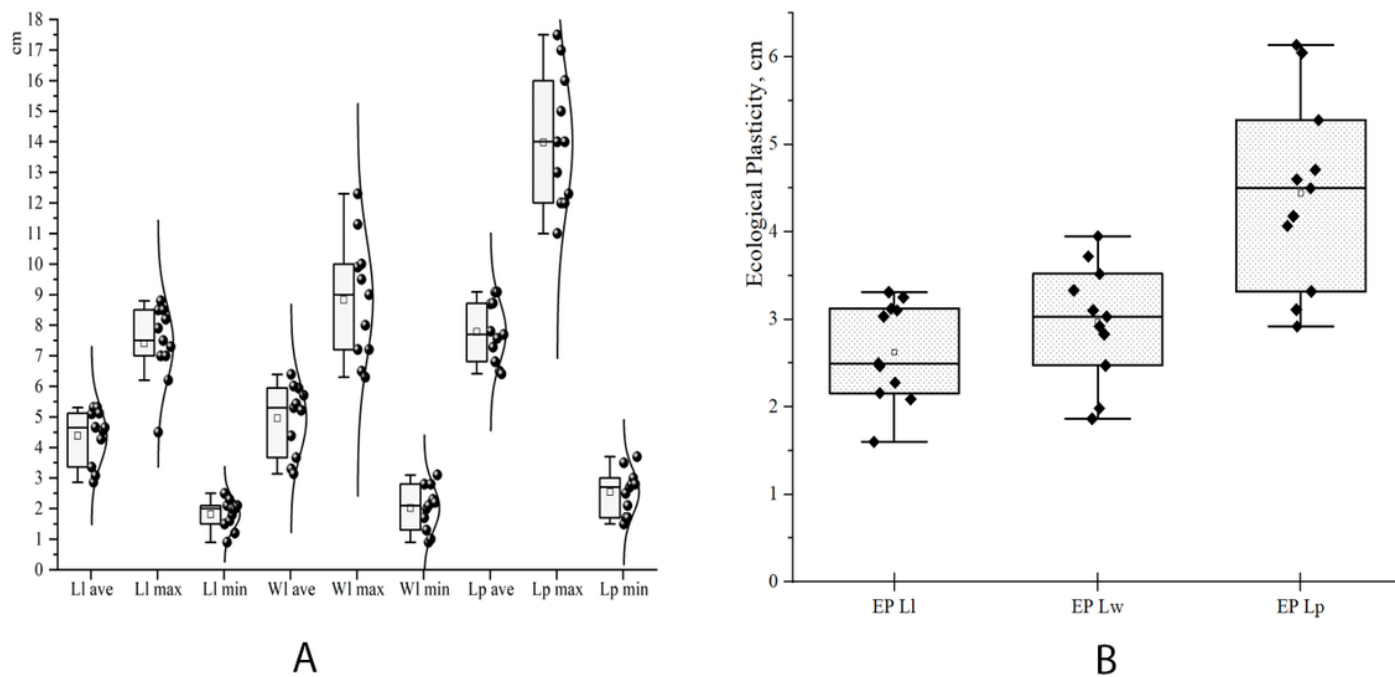


Figure 1

(a): Min, max and average values of morphometric parameters of *H. helix* leaves

(b): Ecological plasticity morphometric parameters of *H. helix* leaves

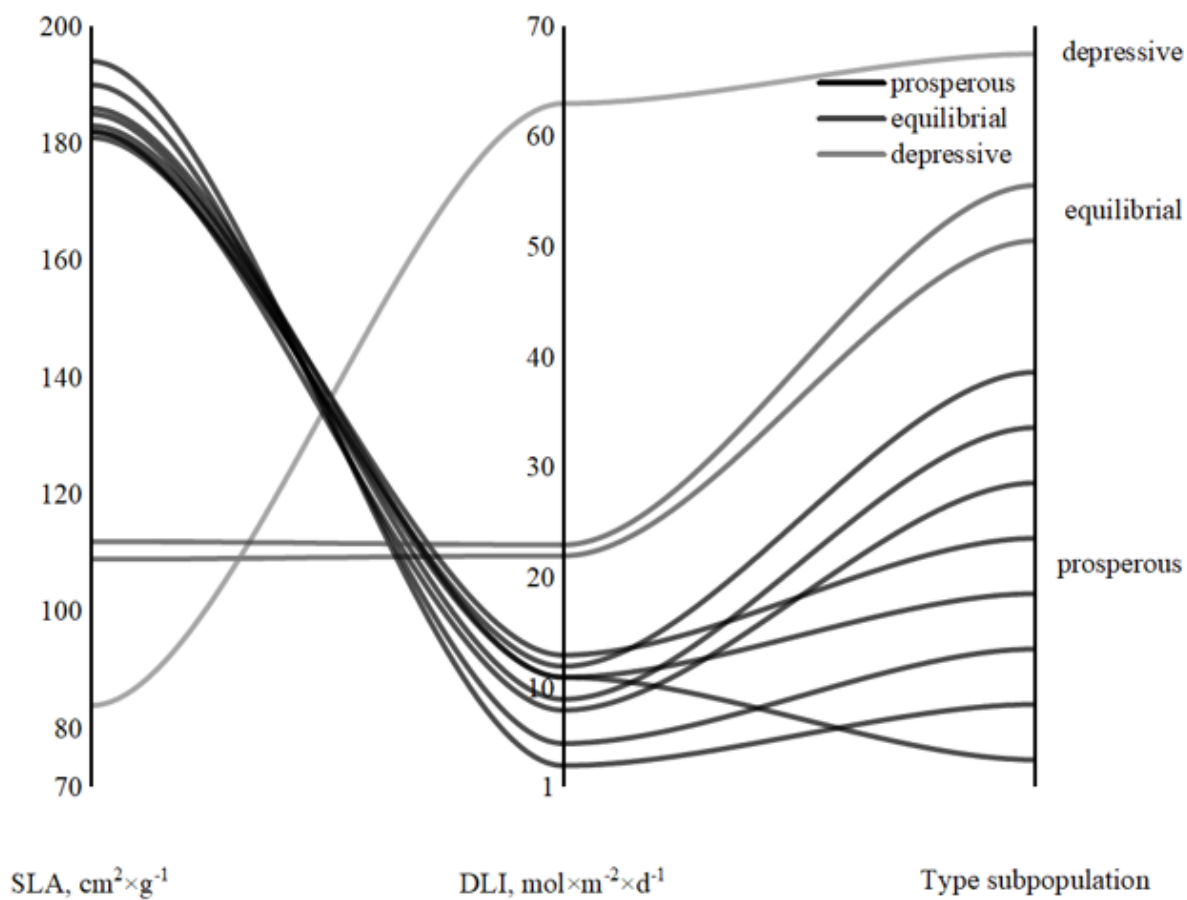


Figure 2

Dependence between DLI, SLA and type of subpopulation of *H. helix*

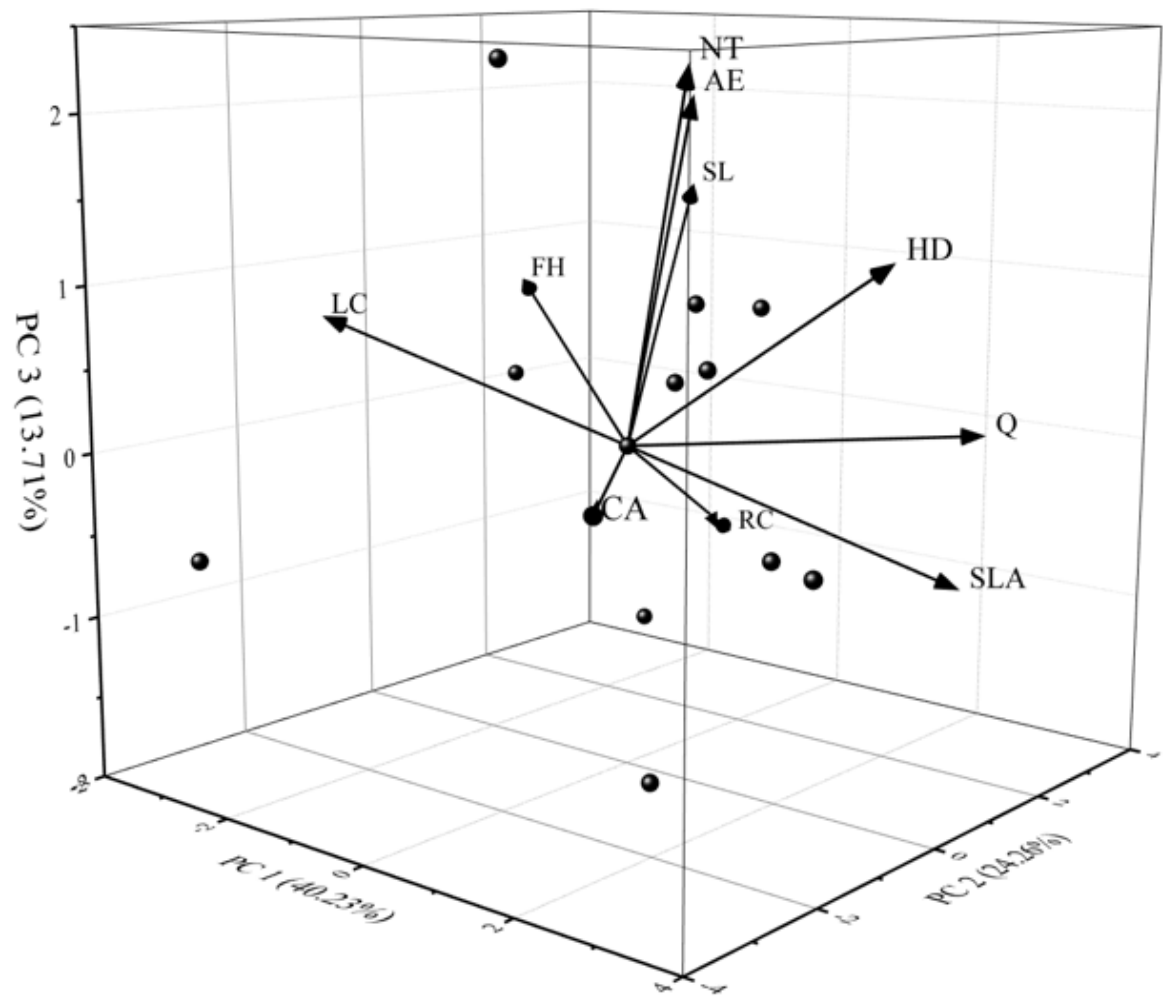


Figure 3

Relationship between phytoindicative values of edaphic factors and SLA/Q

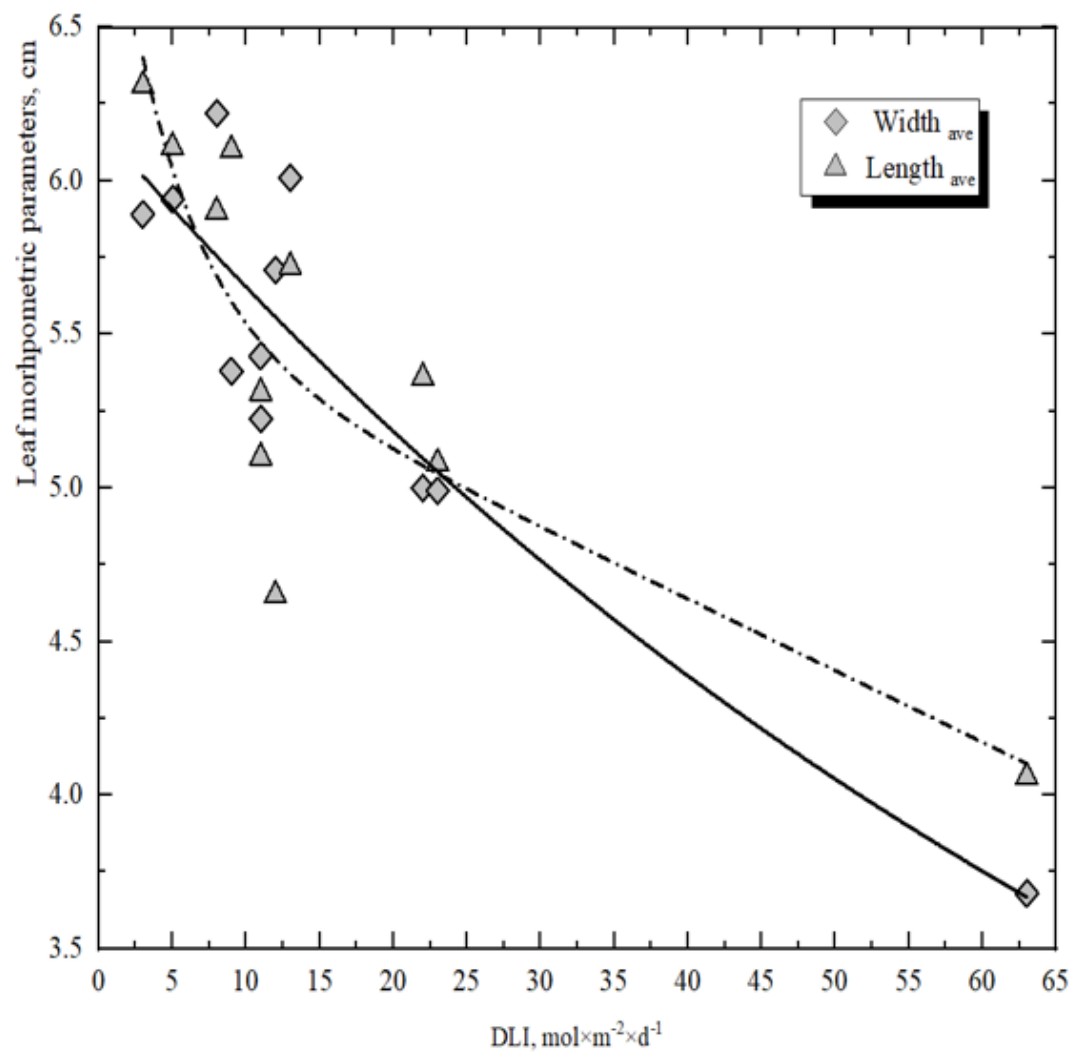


Figure 4

Average values of width and length of leaves of *H. helix* and DLI

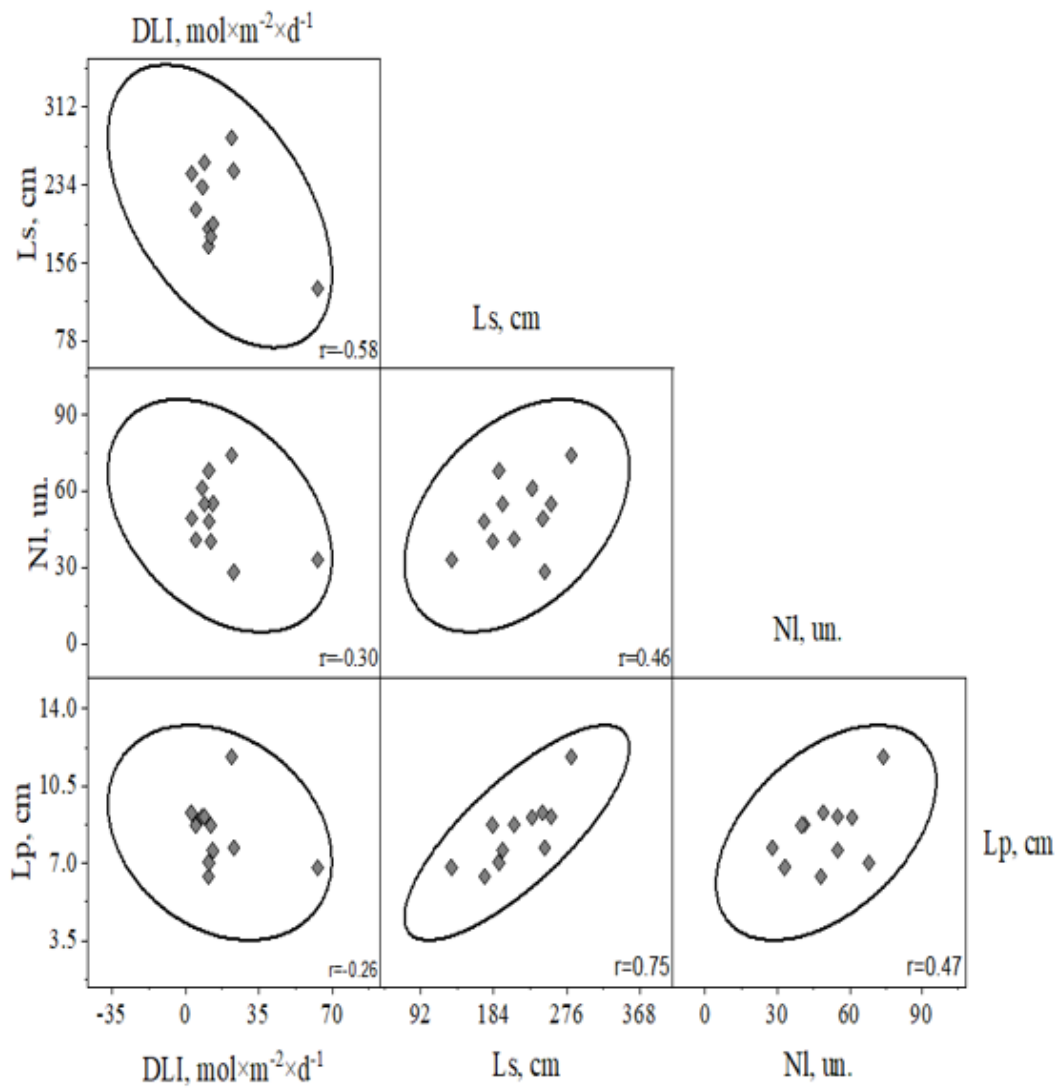


Figure 5

Dependence of morphological parameters of individuals of *H. helix* and DLI

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterial.docx](#)