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ORIGINAL RESEARCH ARTICLE

The trophic requirements of selected underwood species occurring in forests

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Abstract. The subject of this study were soil requirements of common woody shrubs, which may be part of the forest understory (*Sorbus aucuparia* L., *Frangula alnus* Mill., *Corylus avellana* L., *Juniperus communis* L., *Padus avium* Mill., *Euonymus europaea* L., *Sambucus nigra* L.). We focused on phytocenoses in the vicinity of natural forests in reserves and national parks of Polish lowlands and defined optimal types and subtypes of soil with trophic variations for each underwood species. The range of trophism for each species of shrub was determined using specific physico-chemical properties of the soils, while soil quality was assessed using the Trophic Soil Index (SIG) (Brożek et al. 2011a). The ecological requirements of the before-mentioned underwood species were linked with forest typology as well as natural vegetation and they showed different soil requirements. Here we report significant differences in particle size and dynamics of organic matter decomposition in soils associated with these underwood species.

Key words: forest shrubs, soil requirements, forest sites, plant communities

1. Introduction

Shrubs are an important component of forest ecosystems playing primarily biocenotic and phytomelioration functions. As part of the underwood, forest shrubs increase the natural pruning of trees, improve the conditions of the decomposition and enrichment of forest litter, and protect the soil against drying out and overgrowth (Gil 2010). The results of site studies show that shrub species undoubtedly add to the intensification and acceleration of nutrient cycling in the forest ecosystem. Their deep roots and nutrient uptake from deep soil horizons help diversify the quality of the organic matter brought to the soil surface and enhance the biological activity of the soil. At the same time, shrub species seem to be underestimated in the diagnosis of forest sites. In site identification, much more attention is given to the species composition of forest overstory, tree growth and forest floor vegetation (Instruction on Forest Management 2012). This may be the result of a poor knowledge of site requirements of shrub species. In the manuals or lexicon on shrub species, the emphasis is placed primarily on their distinctive features, growth and development characteristics, while site requirements are given much less attention, and their description being often reduced to a few general data on the quality of soils and sites.

This study is intended to fill this gap. Specialist literature lacks a holistic and comprehensive approach to the issue of soil and site requirements of shrub species. There are three groups of studies that contain incomplete, fragmentary data on the issue in question. The first are dendrochronological studies and lexicon on tree and shrub species that comprise only references to the ecological and site (including soil) requirements of individual shrub species. Brief descriptions of these requirements, such as 'soil moderately dry to fresh – all permeable, nutrient-rich, humus soil types, acidic to slightly alkaline' (Bärtels 2011) only mention soil moisture characteristics, its trophism and pH range. The second group consists of instructions and manuals on silviculture, providing more information

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about the preferences of certain shrub species to forest site types (site classification units). They contain data on the ecological amplitude of certain shrub species, but their soil requirements are discussed in very general terms or are even ignored (Ecological basis of silviculture 2004; Jaworski 2011). The third group of studies includes publications and phytosociological manuals that, in the framework of phytocoenosis characterisation, provide information on shrub species and their interactions with natural plant associations (Matuszkiewicz et al. 2012). The knowledge of site conditions, in which certain phytocoenoses develop, allows anticipating the trophic requirements of shrub species. This study describes the soil conditions in which the selected shrub species grow, forming the understory of forest stands. The species were selected on the basis of their frequency under the forest canopy making up the most important forest associations in the lowland and upland areas in Poland. It can be assumed that other shrub species are less numerous in the stands or in open spaces in this area, creating different, non-forest communities, e.g. scrub communities (class *Rhamno-Prunetea*).

The aim of the study is to depict trophic requirements of the selected species of shrubs, defining their site preferences and interactions with forest associations. The subject of the research was soil requirements of common shrub species that can form the forest understory. The study investigates soil requirements of rowan (*Sorbus aucuparia* L.), buckthorn (*Frangula alnus* Mill.), hazel (*Corylus avellana* L.), common juniper (*Juniperus communis* L.), bird cherry (*Padus avium* Mill.), European spindle (*Euonymus europaea* L.) and black elder (*Sambucus nigra* L.).

2. Materials and methods

The study was based on the results of the research conducted on 250 model site plots. The plots had been established in nature reserves and national parks in the Polish lowlands representing the most important forest associations and forest site types. Samples were collected during the implementation of the research project 'The development of soil quality indices for natural forest sites of the Polish lowlands and uplands and their application in forest management'. The research material was collected in 2009–2010. A detailed description of the vegetation representing well-preserved phytocoenoses, under which all forest layers including the understory were characterised, as well as an inventory of the forest floor vegetation was made for each 0.25 ha study plot. Forest plant associations were determined according to the classification by Matuszkiewicz (2001). A detailed methodology for identifying plant associations was presented by Brożek et al. (2011b). Basing on selected geological and soil elements, forest floor vegetation and species composition, each study plot was assigned to an appropriate sites unit – forestsite type. In the central part of the plot, a deep pit was dug from which soil samples were taken from each separated genetic horizon. Particle composition was determined in the soil samples using Bauyoucos-Casagrande's aerometric method modified by Prószyński, soil pH by the potentiometric method in water and in 1 M KCl, hydrolytic acidity by Kappen's method, total nitrogen and carbon contents using a LECO instrument, and alkaline cation content in 1 M ammonium acetate. The types and subtypes of soils were established according to the 'Classification of Polish Forest Soils' (2000). The description of soil conditions for individual shrub species was made on the basis of soil subtypes and selected soil parameters characterising soil quality (total content of clay fraction in the soil, the content of base cations, the degree of soil acidity or the degree of decomposition of humic substances). The content of the selected components was expressed in the volume recalculated to the actual volume of soil column with a cross-section of 1 m^2 and a depth of 150 cm. The described properties were also used to calculate the Trophic Soil Index (SIG), an indicator used in the assessment of soil quality (Instruction on Forest Management 2012; Brożek et al. 2011a; Lasota et al. 2011).

3. Results

This section describes soil and habitat site conditions in which the selected shrub species have developed as well as the relationships between these shrub species and forest communities.

European rowan (*Sorbus aucuparia* L.) is one of the shrubs occurring in our forests with the smallest trophic requirements. It can grow even on the dystrophic Podzols with a low content of nutrients and clay fraction substances (Table 1). Its optimal growth conditions are Haplic Podzols (Bw) and Gleyic Podzols (Bgw) of fresh mixed and moderately moist coniferous forest sites. The content of base cations in these soils is only 2.0–160.0 mols per 1.5 m^{-3}, and the content of clay fraction (<0.02 mm) is usually very low and ranges from 30 to 300 kg per 1.5 m^{-3}. Its preference for such soils is well expressed by the median of the analysed soil parameters given in Table 1.

Concerning the soil subtypes on which the examined shrub species develops, it is easier to identify in the analysed group soils in which the examined shrub species does not grow. These are eutrophic soils containing calcium carbonate – Dystric Gleysols (CZwy) and Calcaric Regosols (PRw), and also the most fertile of the hydrogenic soils – Histic Gleysols (Gmł), Mollic Gleysols (Gp), Fluvisols and soil developed from gyttja (Table 2). The absence of rowan on these soils should be attributed to the competition of other shrub and tree species growing robustly under such conditions rather than to environmental requirements. Analysing the preferences of rowan for specific plant associations, its permanent presence in the mixed forests should deserve attention (*Querco roboris-Pinetum typicum, Querco roboris-Pinetum molinietosum, Querco-Piceetum, Abietetum polonicum*). It is a species strongly favouring the boreal spruce forests on peat soils (*Sphagno girgensohnii-Piceetum*). Furthermore, rowan can be found in the understory of acidophilus deciduous forests (*Luzulo pilosae-Fagetum, Calamagrostio arundinaceae-Quercetum*); it rarely occurs in the continental fresh coniferous forests (*Peucedano-Pinetum*), sub-continental oak forests (*Potentillo albae-Quercetum*), lowland beech forests (*Galio odorati-Fagetum*) and on wet sites in ash-alder forests (*Fraxino-Alnetum*). Surprisingly, this species does not occur in hornbeam forest communities (the collected data set indicates a sporadic occurrence of this species in *Tilio-Carpinetum abietetosum* forests).

Alder buckthorn (*Frangula alnus* Mill.) can be classified as a very tolerant shrub species in terms of soil trophism. Like European rowan, alder buckthorn can grow on dystrophic Podzols, but its optimal growth conditions are pretty wet and highly wet soils. It forms a thick underbrush layer on Gleyic Podzols (Bgw), Haplic Stagnosols (OGw), Histic Stagnosols (OGSt), Hemic Histosol (Dranic) (Mt), Mollic Gleysols (MRw) and Histosols. It is not sensitive to soil acidification and there-

Table 1. Selected parameters of soils inhabited by described shrub

Species	Statistics	Resource of fraction <0.02 mm	Base cations	Acidity recalculated	N^2/C (in humus-mineral horizon)	SIG (Trophic Soil Index)
		kg·1.5 m^{-3}	mol·1.5 m^{-3}	mol Y/kg*		
Sorbus aucuparia L.	min.	0	1,7	0.037	0.0003	6
	max	906	543	4.456	0.0315	38
	median	137.7	32.8	0.358	0.0074	25
Frangula alnus Mill.	min.	0	1.2	0.098	0.0003	4
	max	585.1	490.6	82.345	0.0406	34
	median	56.5	31.1	1.031	0.0066	20
Corylus avellana L.	min.	0	2.7	0.006	0.0016	14
	max	1516.4	965.5	8.699	0.0362	40
	median	145.6	116.4	0.242	0.0124	32
Juniperus communis L	min.	16.6	1.6	0.235	0.0003	4
	max	302.4	238.1	3.106	0.016	32
	median	58	3.3	0.809	0.0024	13
Padus avium Mill.	min.	0	25.7	0.049	0.0075	24
	max	625.4	584.1	8.699	0.0366	38
	median	99.7	123.1	0.225	0.0215	32
Euonymus europaea L.	min.	29.7	5.1	0.006	0.0019	15
	max	1516.4	965.5	1.265	0.0362	40
	median	311.8	162.9	0.128	0.0151	34
Sambucus nigra L.	min.	0	81.1	0.006	0.0018	27
	max	1516.4	965.5	0.276	0.0471	40
	median	459.2	269.5	0.088	0.0172	35

* of fraction <0.02 mm

Table 2. The subtypes of soils inhabited by tested shrubs species (in bold marked the preferred soil subtypes, presenting optimal conditions for growth)

Soil type	*Juniperus communis* L.	*Sorbus aucuparia* L.	*Frangula alnus* Mill.	*Corylus avellana* L.	*Euonymus europaea* L.	*Padus avium* Mill.	*Sambucus nigra* L.
ARw	x						
Bw	x	x	x				
Bgw		x	x				
RDb	x	x	x	x	x		
RDw	x	x	x	x	x		
RDbr	x	x	x	x	x	x	x
BRb		x	x	x	x		
BRk		x	x	x	x	x	x
BRwy		x	x	x	x	x	x
BRw		x		x	x	x	x
BRs		x		x	x	x	x
PRbr				x	x	x	x
PRw				x	x	x	x
Pb		x		x			
Pw		x		x	x	x	x
Pog		x	x	x	x	x	x
OGb	x	x	x	x			
OGw	x	x	x	x	x	x	x
OGam		x	x	x	x	x	x
OGSt	x	x	x	x			
Gt		x	x	x	x		
Gm		x	x	x	x	x	x
Gts		x	x	x	x	x	x
Gms		x	x	x	x	x	x
Gw		x	x	x	x	x	x
Gp		x	x	x	x	x	x
Gmł		x	x	x	x	x	x
CZwy				x	x	x	x
MRw		x	x	x	x	x	x
MRm		x	x	x	x	x	x
MRms		x	x	x	x	x	x
MDbr				x	x	x	x
MDw				x	x	x	x
MDp				x	x	x	x
MŁw				x		x	x
MŁt			x	x		x	x
Mt			x				
Tw		x	x				
Tp		x	x	x		x	
Tn		x	x	x		x	x

Notes: ARw – Arenosol, Bw – Haplic Podzol, Bgw – Gleyic Podzol, RDb – Albic Brunic Arenosol, RDw – Haplic Brunic Arenosol, RDbr – Cambic Brunic Arenosol, BRb – Albic Cambisol, BRk – Hyperdystric Cambisol, BRwy – Epidystric Cambisol, BRw – Eutric Cambisol, BRs – Cambisol Humic Eutric, PRbr – Calcaric Cambisol Skeletic, PRw – Calacaric Regosol, Pb – Albic Luvisol, Pw – Haplic Luvisol, Pog – Stagnic Luvisol, OGb – Albic Stagnosol, OGw – Haplic Stagnosol, OGam – Haplic Stagnosol, OGSt – Histic Stagnosol, Gt – Histic Gleysol, Gm – Histic Gleysol, Gts – Histic Gleysol, Gms – Histic Gleysol, Gw – Haplic Gleysol, Gp – Mollic Gleysol, Gmł – Histic Gleysol, CZwy – Dystric Gleysol, MRw – Mollic Gleysol, MRm – Gleysol Abruptic, MRms – Histosol, MDbr – Cambic Fluvisol, MDw – Gleyic Fluvisol, MDp – Mollic Fluvisol, Młw – Limnic Histosol, MŁt – Fibric Histosol, Mt – Hemic Histosol Drainic, Tw – Fibric Histosol Orthodystric, Tp – Histosol Orthodystric, Tn – Hemic Histosol Eutric fore can thrive on these poorest soil subtypes containing acidic humus. The underlying bedrock is various kinds of sands (especially river sands, glaciofluvial sands, shallow eolian sands) as well as peat. The total content of clay fraction in oligotrophic soils is, in the case of presence of organic sediments, very low, varying from about 30 to 200 kg per 1.5 m^{-3}, provided that these soils are formed on a mineral bedrock. The content of cations in such soils ranges respectively from 2.0 mols per 1.5 m^{-3} in Gleyic Podzols (Bgw) up to 120 mols per 1.5 m^{-3} in Histosols (Orthodystric) (Tp). Should we consider all the soils in which alder buckthorn grows, the range of these parameters becomes respectively wider. Nevertheless, the median expresses its preference for poorer and more acid soils (Table 1). The soils in which alder buckthorn grows are characterised by one of the least favourable indicators of soil humus decomposition, the N^2/C parameter, being the percent of total nitrogen divided by C/N ratio in the first humus-mineral soil horizon, usually oscillates around 0.006. In the examined group, only the soils under common juniper showed lower value of this parameter. Moreover, only soils in which alder buckthorn grew the least favourable acidity ratio showed, the so-called acidity recalculated, *i.e.* the total acidity divided by the content of clay fraction in the same soil volume. The median value of this indicator exceeds the value of 1.00 (Table 1) only for alder buckthorn which means that, on average, 1 kg of fraction <0.02 mm in the soils under alder buckthorn contains more than 1 mol of acid ions.

Alder buckthorn can grow in various forest associations. It favours moist sub-continental associations of mixed coniferous forest (*Querco roboris-Pinetum molinietosum*), moist pine forest (*Molinio-Pinetum*), bog pine forest (*Vaccinio uliginosi-Pinetum*), bog birch forest (*Vaccinio uliginosi-Betuletum*) and spruce forest on peatbogs (*Sphagno girgensohnii-Piceetum*). It is also a very common shrub in alder carrs (*Sphagno squarrosi-Alnetum*, *Ribeso nigri-Alnetum*). In acidophilus deciduous forests, this species often occurs in more wet sub-associations such as Central-European acidophilus oak forests (*Molinio-Quercetum petraeae*), wet sub-associations of beech-oak forests (*Fago-Quercetum molinietosum*) or sub-continental hornbeam forests with *Carex brizoides* (*Tilio-Carpinetum caricetosum brizoides*).

Common hazel (*Corylus avellana* L.) is another shrub species often encountered in our forests. Compared with European rowan or alder buckthorn, it has slightly higher soil trophic requirements. It basically avoids soils with an advanced podsolisation process. Mesotrophic and eutrophic soils, fresh to highly moist, create advantageous growth conditions for hazel. These are Haplic Brunic Arenosols (RDw), Cambic Brunic Arenosols (RDbr), all sub-types of Cambisols and Luvisols, Stagnosols (especially Haplic Stagnosols (OGw) and Haplic Stagnosols OGam), mesotrophic and eutrophic Gleysols (Haplic Gleysols (Gw), Mollic Gleysols (Gp) and Histic Gleysols (Gms), Dystric Gleysols (CZwy), Calcaric Regosols and Mollic Gleysols (MRw)). As regards highly wet forest sites, common hazel can grow on Limnic Histosols and Histosols – Histosols (Orthodystric) (Tp) and Hemic Histosols (Eutric) (Tn). Unlike the previously discussed shrubs, common hazel prefers soils rich in a fine fraction and base cations. In fresh site soils, the optimum growth conditions for hazel are when the content of clay fraction exceeds 100 kg per 1.5 m^{-3} (in the soils developed from clays, the content of clay fraction is up to 1500 kg per 1.5 m^{-3}). In the soils under the strong effect of groundwater, especially Histosols or Mollic Gleysols, the content of this fraction can be less than 100 kg per 1.5 m^{-3}. The median value of fraction <0.02 mm in the soils in which common hazel grows indicates its preferences for soils with a high content of fine fractions (Table 1). The content of exchangeable cations in the soil under hazel varies greatly; this particularly concerns Arenosols in which the content of base cations ranges widely from 3.0 to 200.0 mols per 1.5 m^{-3}. In Cambisols, Luvisols or Calcaric Regosols where hazel has particularly favourable growth conditions, the content of cations is higher, ranging from 300 to 1500 mols per 1.5 m^{-3}. The semi-hydrogenic and hydrogenic soils, in which hazel grows and in which the contained water increases the availability of cations, contain 20–650 mols per 1.5 m^{-3} of base cations.

The assessment of soils using the acidity recalculated parameter shows that, on average, the soils in which hazel grows are approximately four times less acidic as per unit weight of clay fraction than those under alder buckthorn and common rowan. The level of humus accumulation in soils considered positive for the growth of hazel is characterised by the favourable degree of decomposition and a high content of nitrogen expressed in N:C/N ratio (Table 1).

Analysing the preferences of common hazel for forest site types and forest associations, emphasis should be placed on its preferences for hornbeam associations. About half of the areas occupied by common hazel were covered by various sub-associations of hornbeam forests connected with their regionalisation or trophic level (*Tilio-Tilio-Carpinetum calamagrostietosum, Carpinetum typicum, Tilio-Carpinetum corydaletosum, Galio-Carpinetum typicum, Galio-Carpinetum stachyetosum, Stel-*

lario-Carpinetum, Acer platanoides-Tilia cordata). As regards site types, these are fresh mixed, moist mixed, fresh and moist deciduous forests. Common hazel growing on eutrophic hydrogenic soils is associated with alder carrs (*Ribeso nigri-Alnetum*), ash-alder forests (*Fraxino-Alnetum*), elm-ash forests (*Ficario-Ulmetum minoris*) corresponding to alder carr, ash-alder forest and riparian forest sites. A sporadic occurrence of hazel was also noted in more fertile continental mixed coniferous forests (*Querco roboris-Pinetum*) and subboreal mixed coniferous forests (*Serratulo-Pinetum*), or in the thermophilous oak forests (*Potentillo albae-Quercetum*) (in terms of site, these areas are identified as fresh mixed deciduous forest).

Common juniper (*Juniperus communis* L.) is widely recognised as a species favouring sandy soils. The fact of its occurrence in the understory on the study sites confirms this. Of our native shrubs, common juniper can be regarded as a species of the lowest trophic and soil moisture requirements. It can grow on dry Arenosols or Podzols and Albic Brunic Arenosols (RDb) derived from dune sands. These are barren soils with a low content of both the clay fraction (17–65 kg per 1.5 m^{-3}) and base cations (1.6–11.0 mols per 1.5 m^{-3}), strongly acidic with a low degree of humus decomposition in the form of a mor-humus that lies on the soil surface. Such soils have the lowest Trophic Soil Index (SIG 4–12) value characteristic of dystrophic sites of dry and fresh coniferous forests. Juniper can also grow on sands richer in nutrients, fresh oligotrophic and even mesotrophic soils. In the analysed group of plots, it was found on different subtypes of Albic Brunic Arenosols (RDB), Haplic Brunic Arenosols (RDw) and Cambic Brunic Arenosols (RDbr) developed from glaciofluvial sands and clays, forming a site of fresh mixed coniferous, or even fresh mixed deciduous forests. While assessing soil quality using SIG, the parameters characterising such soils are slightly more favourable, as shown in Table 1. It seems that the limited occurrence of common juniper on more fertile soils is due to the competition from other, more expansive species and the lack of light. Forest associations in which the juniper can be encountered are mainly *Cladonio-Pinetum* forests and fresh pine forests (*Leucobryo-Pinetum, Peucedano-Pinetum*). This species can grow on slightly more fertile sandy soils that are associated with mixed coniferous forests (*Querco roboris-Pinetum, Serratulo-Pinetum*) and the poorest forms of hornbeam forests (*Tilio-Carpinetum calamagrostietosum*) or thermophilous oak forests (*Potentillo albae-Quercetum*).

Bird cherry (*Padus avium* Mill.) is a shrub of meso-eutrophic wet and marshy soils. The analysed material shows that bird cherry prefers soils with flowing water, avoiding sites with stagnant water. It grows well on a variety of subtypes of Fluvisols (Gleyic Fluvisols (MDw), Cambic Fluvisols (MDbr), Mollic Fluvisols (MDp)). In the valleys with slow-flowing streams and rivers, bird cherry occupies Histic Gleysols (Gt, Gm, Gms), Mollic Gleysols (MRw) and Dystric Gleysols (CZwy) (Table 2). It tolerates the stable high water level provided that water is flowing and is rich in nutrients. Such conditions favour the formation of deep Histosols (Orthodystric) (Tp) and Hemic Histosols (Eutric) (Tn), and in the case of over-drying Hemic Histosols (Drainic) (Mt). Bird cherry is rarely encountered on less wet soils, like Cambisols, Arenosols or Regosols. Without any exception, these are areas adjacent to flooded valleys or to the terrains containing the above-mentioned soils (contact zones of fresh sites with areas that remain under the effect of flowing water) or currently drained areas that previously remained under the influence of such water. The quality of soils in which bird cherry grows is described by the value of SIG (24–38, median 32). The content of clay fraction in the soils under bird cherry is highly variable and depends on the amount of the accumulated organic matter. Deep peat soils do not contain clay fraction, while heavy, fine-grained Fluvisols or Cambisols contain more than 600 kg of clay fraction per 1.5 m^{-3}. The content of base cations in the soils in which bird cherry grows is high (more than 120 mols per 1.5 m^{-3}); however, the presence of flowing water makes the actual content and availability of base cations in the soils even higher, compared with the result obtained when earth fraction samples alone are identified. The content of nitrogen expressed as the C:N (N^2/C) ratio is indicative of the high trophic level of soils occupied by the discussed shrub species. The average value of this indicator in the mineral horizons of soils preferred by bird cherry exceeds 0.02. The presence of water rich in base cations indicates low acidification of the examined soils, as shown by the acidity value (Y_p) – the median is 0.225 (Table 1).

The preferences of bird cherry for the above-described fertile soils limit the spectrum of forest associations in which this species grows. In the case of alluvial soils, these are various riparian forests (*Salici-Populetum, Ficario-Ulmetum minoris, Fraxino-Alnetum*), and in the case of Histosols or Hemic Histosols (Drainic) (Mt), bird cherry occurs in ash-alder forests (*Fraxino-Alnetum*), less rarely in alder swamp forest (*Ribeso nigri-Alnetum*). In the case of mineral soils, Cambisols Gleyic, bird cherry is found in the understory of wet hornbeam sub-associations (*Tilio-Carpinetum corydaletosum, Tilio-Carpinetum abietetosum*) or wet *Mercuri-Fagetum* beech forest sub-association.

European spindle (*Euonymus europaea* L.): The analysed material shows that European spindle requires meso-eutrophic soils. Isolated cases of its occurrence in the understory have already been found on fertile Arenosols of fresh mixed deciduous and fresh deciduous forest sites. A larger number and more robust growth of spindle is observed on eutrophic soils: Cambisols (especially Epidystric Cambisols (BRwy) and Eutric Cambisols (BRw)), Luvisols, Regosols as well as on wet, fertile alluvial Fluvisols, Gleysols and Stagnosols (Table 2) that provide optimal growth conditions for this shrub species. The research did not confirm the occurrence of spindle in highly acidic soils with the ongoing podsolisation process and on organic soils with stagnant water causing swamping. As regards soil texture, the dominant soils occupied by spindle are heavy soils with a high content of clay fraction (from approximately 200 to over 1500 kg per 1.5 m^{-3}) and base cations (from 70 to 1000 mols per 1.5 m^{-3}). The exception are few sandy, Arenosols, Gleysols and Stagnosols in which clay particles can be below 100 kg per 1.5 m^{-3}, and base cations below 40 mols per 1.5 m^{-3}. Due to the fact that the land occupied by spindle is characterised by mull or moder-mull type of humus, the accumulation horizons of humus are characterised by a high degree of decomposition of organic matter that is reflected in the values of N^2/C parameter (0.0044–0.0362, median 0.0151) (Table 1). The low acidity and high content of clay fraction in the soils under spindle makes parameter Y_p assume positive low values (average 0.128 mol of hydrogen ions/kg of clay fraction), which are among the most favourable in the soils occupied by the studied shrub species.

Because of its soil requirements, spindle favours fresh and moist meso-eutrophic sites. Forest associations in which it occurs primarily includes sub-associations and varieties of hornbeam forests (subatlantic hornbeam forests – *Stellario-Carpinetum typicum*; Central-European hornbeam forests – *Galio-Carpinetum typicum, Galio-Carpinetum stachyetosum*; sub-continental hornbeam forests – *Tilio-Carpinetum calamagrostietosum, Tilio-Carpinetum typicum, Tilio-Carpinetum corydaletosum*, *Acer platanoides-Tilia cordata* hornbeam forests), riparian forest associations (*Salici-Populetum, Ficario-Ulmetum minoris, Fraxino-Alnetum*) as well as beech forests (*Mercuri-Fagetum*).

Black elder (*Sambucus nigra* L.) is one of the shrubs with the highest soil requirements. The carried out research shows that black elder occurs almost exclusively on eutrophic soils including the most fertile Cambisols (Epidystric Cambisols (BRwy), Eutric Cambisols (BRw), Cambisols (Humic Eutric) (PRw)), Luvisols, Haplic Stagnosols (OGw), Haplic Gleysols (Gw), Calacaric Regosols (PRw), Dystric Gleysols (CZwy), Phaeozems and Fluvisols (Table 2). When it occurs on mesotrophic soils, these are exclusively areas adjoining eutrophic riparian sites (edges of moraine plateaus adjacent to river valleys) or drained river valleys. In terms of moisture content, these are fresh and highly moist soils. On swampy soils, black elder requires flowing and oxygenated water. The soils that meet such requirements are Histosols accumulated in the valleys of small streams and rivers. The high trophism of soils under black elder stems from the high content in these soils of clay fraction, exchangeable base cations, humic substances and often calcium carbonate. Table 1 shows selected characteristics of soils preferred by black elder. Obviously, the differences in the fertility of the examined soils should be explained by their origin. In addition to river valleys where soil fertility is determined by a steady supply of nutrients from water, and where Fluvisols and Histosols less abundant in clay fraction can accumulate, black elder favours heavy soils abundant in clay fraction (containing >300 kg of fraction <0.02 mm per 1.5 m^{-3}). A common feature of soils occupied by black elder is the high content of well-decayed humus and low acidity (of the analysed shrubs, black elder grows on soils with the most favourable (lowest) acidity index expressed by the ratio of total acidity to clay fraction content in a soil pedon of 1.5 m^3). The mean value of Y_p in the soils under black elder is below 0.1 mol of acidity/kg of fraction <0.02 mm.

Due to its preference for fertile soils and eutrophic sites, black elder can form the understory in typical and wet hornbeam forest sub-associations (*Stellario-Carpinetum typicum*, *Galio-Carpinetum typicum, Galio-Carpinetum stachyetosum*, *Tilio-Carpinetum typicum, Tilio-Carpinetum abietetosum, Tilio-Carpinetum corydaletosum*, *Acer platanoides-Tilia cordata*), riparian forests (*Ficario-Ulmetum minoris, Fraxino-Alnetum*) and alder carrs (Ribeso nigri-Alnetum) and even in beech forests (*Mercuriali-Fagetum*).

The preparation of characteristics of soil conditions in which shrub species in question can grow allowed determination of a range of habitats providing the most favourable (optimal) growth conditions that should be taken into consideration while selecting species able to form the underwood (Table 3). This knowledge can also be used in the assessment of the productive capacity of forest sites, especially when species composition of the overstory is unadjusted to habitat conditions and does not fully reflect 'forest productive capacity'. The growth of shrubs requiring mesotrophic or eutrophic sites and soils under pine forests is an undeniable sign of the earlier forest management; however, it should not be regarded as a manifestation of 'eutrophication of sites', but as a natural process of restoration of the natural diversity and species-richness of phytocoenosis. The shrub species in question have different soil requirements that can be determined by an optimum-conditioning robust growth, by preferences for the selected factors and by lack of tolerance for other soil and site conditions.

4. Discussion

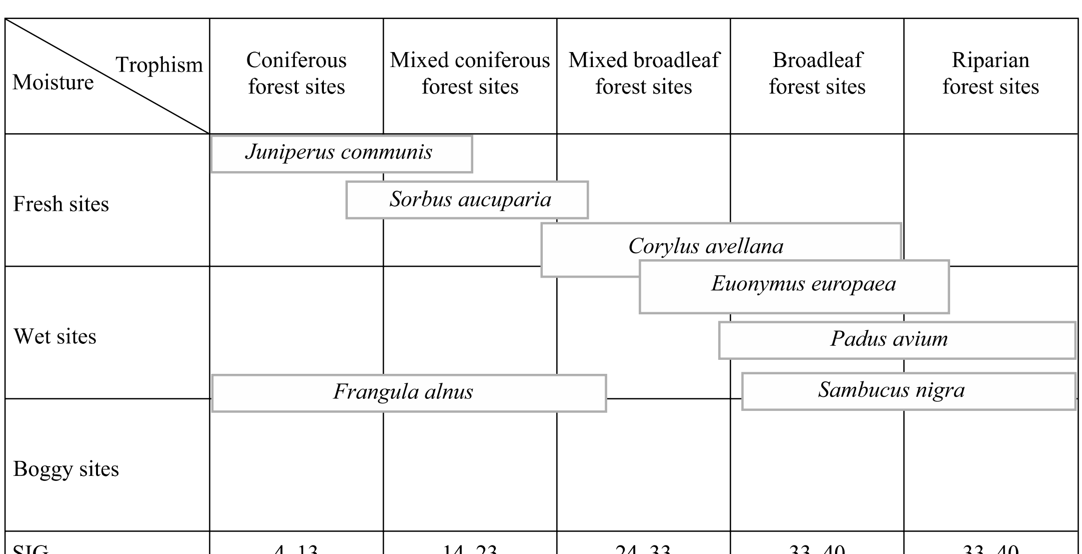
The obtained results largely confirm the opinion prevailing in literature about the requirements of individual shrub species. The tolerance of juniper to nutrient-poor, dry sandy soils and its preferences for dry and fresh pine forest sites has long been known (Tomanek 1951; Seneta, Dolatowski 1997; Bolliger et al. 1998). The presented results also confirm the possibility of juniper growth on both the poorest and driest forest soils in their initial stage of development (sandy, dry arenosols) as well as on Podzols derived from deep aeolian sands. The growth of juniper on such dystrophic soils, however, does not necessarily mean that it cannot be used as an underwood species in oligotrophic and mesotrophic soils and sites. It is likely that in thinned stands composed of pine and oak, juniper can form underwood on all the soils developed from sands of various origins (including glacial sands).

Information on low requirements of rowan can also be found in the dendrochronological studies (Godet 1997; Seneta, Dolatowski 1997).

Rowan is considered one of the least demanding, site-tolerant shrub species. The presented material basically confirms this opinion, as it is easier to identify soil types on which rowan does not occur in the understory. However, it is impossible to agree fully with the study by Godet (1997) according to which rowan does not tolerate sites with a permanent and excessive moisture content. Also, Jaworski (2011) in his research on the ecological requirements of this species indicates that rowan does not at all occur on boggy, alluvial and peat soils. The presented results contradict these opinions and suggest the possibility of rowan to grow on peat soils, especially in the boreal spruce forest association (*Sphagno girgensohnii-Piceetum*) in north-eastern Poland and marshy soils in ash-alder carrs (*Fraxino-Alnetum*). The possible occurrence of rowan in mixed bog coniferous forest sites is described in the study by Puchniarski (2004) that is consistent with the results of this study.

Alder buckthorn is a shrub that undoubtedly is associated with dystrophic and oligotrophic soils. The conducted research indicates that this species prefers wetter soils – Gleyic Podzols (Bgw) and strongly acidified Histosols. Of the analysed shrubs, alder buckthorn is the species tolerating the highest soil acidification. Bolliger et al. (1998) emphasise its preferences for moist soils, though it is difficult to agree with the opinion of these authors that

Table 3. Site conditions under which shrubs find optimal conditions for growth



these moist soils should be loams or sandy loams. The results presented in this study show that alder buckthorn does not require soils abundant in clay fraction. On the contrary, it can thrive on soils associated with dystrophic and oligotrophic sites with a texture of loose sands with a low clay content where the total content of fraction <0.02 mm is only 30–100 kg per 1.5 m^{-3}. The preferences of alder buckthorn for such moist or even bog forests, moist mixed coniferous forests, mixed coniferous-deciduous bog forests or moist mixed deciduous forests are also highlighted in the study by Puchniarski (2004).

Somewhat contradictory information on soil and site requirements of common hazel can be found in literature. According to Bolliger et al. (1998), it is a species preferring calcareous soils, but can also be encountered on neutral and humus soils. Jaworski (2011) indicates slightly larger differences in the soil conditions in which this species grows. The author states that common hazel favours mineral and humus soils rich in calcium carbonate, but it also grows on acid and neutral soils. In the light of the presented results, it seems unfortunate to associate common hazel with a very wide range of trophism of forest sites – from mixed coniferous to deciduous forests (Ecological basis of silviculture 2004; Puchniarski 2004; Matuszkiewicz et al. 2012). This is probably the result of confusing an erroneous association of the continental mixed coniferous communities with hazel (*Querco roboris-Pinetum coryletosum*) with oligotrophic sites identified in the typology of forest sites. The results of the research by forest site specialists (Sikorska, Lasota 2007) indicate that *Querco roboris-Pinetum coryletosum* should be associated with mesotrophic and even eutrophic sites, while phytocoenosis should be treated as a substitutional community that has formed as a result of promoting planting pine species in fertile soils under hornbeam forests. site requirements of hazel were defined in a very accurate and concise manner by Seneta and Dolatowski (1997) who demonstrated that site requirements of this species were similar to those of hornbeam, but it avoided barren, dry and wet soils. The analysis of the material presented in this study confirms hazel's preferences for the sites of hornbeam forest associations growing on mesotrophic and eutrophic soils, mixed deciduous forests as well as fresh and moist deciduous forests.

The results from the research show that spindle, bird cherry and black elder are soil and site-demanding species. They are typical of eutrophic sites differing in certain specific requirements regarding soil moisture, the kind and duration of water impact as well as topography. According to Bolliger et al. (1998), spindle favours fertile, highly wet, deep loamy soils containing calcium under deciduous and riparian forests. Jaworski (2011) defines humus, fresh and calcium-rich soils as favourable for the growth of spindle. The performed research did not confirm spindle's preferences for soils rich in calcium carbonate. The occurrence of spindle in the forest understory was already recorded in more nutrient-richer rusty soils of mixed fresh and fresh deciduous forest sites. Cambisols were found to be optimal for the development of this species (especially Epidystric Cambisols (BRwy) and Eutric Cambisols (BRw)) – Luvisols and Regosols. It also favours wet, eutrophic alluvial soils – Gleysols and Stagnosols However, it was demonstrated that this shrub species does not occur in strongly acidified, podsolised soils and boggy organic soils – Histosols. Fine-grained soils with a high content of fraction <0.02 mm and base cations dominate in the granulometric composition of soils in which spindle grows.

Information on bird cherry requirements found in literature is scarce. Amann (1954) describes bird cherry as a species requiring heavy humus soils from fresh to wet. Seneta and Dolatowski (1997), Gil (2010) and Matuszkiewicz et al. (2012) link this species to wet deciduous forests and riparian vegetation as well as to wet hornbeam forests and alder carrs. Jaworski (2011) describes the soils preferred by this species as moist, fertile loamy soils with neutral and alkaline pH. The present study indicates that bird cherry particularly favours soils with moving, flowing water. A good growth of this shrub species was observed on different subtypes of Fluvisols, while in the valleys with slow-flowing streams and rivers it grows on Histic Gleysols (Gt, GM, Gms), Dystric Gleysols (CZwy), Mollic Gleysols (MRw) and Histosols (MRms). It tolerates a permanently high water level, provided that the water is flowing and is rich in nutrients. Soil requirements of black elder are very similar to those of bird cherry, and in literature it is considered a calcium- and nitrogenphilous species (Seneta, Dolatowski 1997; Gil 2010). Jaworski (2011) indicates that black elder is not a demanding species, although it best grows on fertile humus soils, tolerating slight salinity, and often occurs on calcium-rich soils. The presented results indicate the preferences of black elder for eutrophic soils. Such soils are the most fertile subtypes of Cambisols (Epidystric Cambisols (BRwy), Eutric Cambisols (BRw), Cambisol (Humic Eutric) (BRs)), Luvisols, Haplic Stagnosols (OGw), Haplic Gleysols (Gw), Calacaric Regosols (PRw), Dystric Gleysols (CZwy), Phaeozems and Fluvisols.

A good knowledge of soil requirements of shrubs allows their use in the diagnosis of forest sites. It seems that these plants are underestimated in site studies, whose purpose is identification and mapping of forest areas differing in their production capabilities. The instruction for the identification and mapping of sitess (2012) specifies forest floor vegetation and stand characteristics as floristic indicators useful in site identification, of which species composition of stand overstory and productivity of the main forest tree species are considered to be most important. While the Ecological Basis of Silviculture (2004) provide a list of shrub species in different types of forest sitess, they point to the ecological amplitude of shrub species rather than the optimal conditions in which these species can flourish to form the understory.

5. Summary

As a result of assigning soil and site trophism to the requirements of the examined shrub species, the following sequence of species was established: common juniper, alder buckthorn – dystrophic to oligotrophic soils and sites, European rowan – oligotrophic to mesotrophic sites, common hazel, European spindle – mesotrophic to eutrophic sites, bird cherry, black elder – eutrophic sites.

The requirements of each shrub species with respect to soil moisture and type of water are arranged in the following order: common juniper – dry to fresh soils, European rowan, common hazel, European spindle – fresh to moderately wet soils, bird cherry – moderately to highly wet, waterlogged soils containing rainfall water, or being periodically inundated, black elder – moderately wet to very wet soils with moving, flowing water, or periodically inundated, spindle – moderately wet to marshy soils with stagnant acidified water.

Common juniper is among the most tolerant shrubs under consideration, it grows well even on dry Podzols or Arenosols formed from deep dune sands. Its high tolerance results from drought resistance, which goes along with relatively large high light requirements.

Alder buckthorn prefers wet soils and tolerates strongly acidic environments indicating its preference for Gleyic Podzols (BGw), Hemic Histosol (Drainic) (Mt) and less fertile Stagnosols, Gleysols. It well tolerates soil swamping. It does not require a high content of clay fraction, and grows well on sandy soils, provided they are sufficiently wet.

Rowan is a very plastic species with wide ecological amplitude. Being resistant to soil acidification, it is associated primarily with mixed coniferous forest sites and communities in pine, oak-pine, spruce-pine and fir forests. It does well already on podzolic and rusty soils of different subtypes.

Common hazel is a shrub favouring hornbeam forest sites, growing well on soils abundant in clay fraction, developed from boulder clay, silt loam of aquatic origin and lithological discontinuities – sands underlain by compact soils (dust, loams or clay soils). These are mainly Cambisols and Luvisols, and nutrient-richer soil Stagnosols and Gleysols and Calacaric Regosols. It does not grow on strongly acidified soils undergoing a podsolisation process.

Bird cherry particularly favours riparian forest soils and sites with flowing water. The soils that are most favourable for the growth of this shrub species include fluvisols in the valleys of large rivers, and Histic Gleysols (Gt, Gm, Gms), Mollic Gleysols (MRw) and Dystric Gleysols (CZwy) in the valleys of slow-flowing streams and small rivers.

The soil requirements of black elder are very similar to those of common bird cherry, growing well on all fertile soils containing well-decomposed, nitrogen-rich mull humus (fertile Cambisols, Luvisols, Stagnosols, Gleysols, Regosols, Phaeozems and Fluvisols).

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