Impact of secondary succession in abandoned fields on some properties of acidic sandy soils

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Abstract: Abandonment of agricultural lands in recent decades is occurring mainly in Europe, North America and Oceania, and changing the fate of landscapes as the ecosystem recovers during fallow stage. The objective of this study was to find the impact of secondary succession in abandoned fields on some parameters of acidic sandy soils in the Borská nížina lowland (southwestern Slovakia). We investigated soil chemical (pH and soil organic carbon content), hydrophysical (water sorptivity, and hydraulic conductivity), and water repellency (water drop penetration time, water repellency cessation time, repellency index, and modified repellency index) parameters, as well as the ethanol sorptivity of the studied soils. Both the hydrophysical and chemical parameters decreased significantly during abandonment of the three investigated agricultural fields. On the other hand, the water repellency parameters increased significantly, but the ethanol sorptivity did not change during abandonment. As the ethanol sorptivity depends mainly on soil pore size, the last finding could mean that the pore size of acidic sandy soils did not change during succession.

Keywords: Water repellency; Acidic sandy soil; Land abandonment; Secondary succession; Soil properties.

INTRODUCTION

Farmland abandonment in recent decades (with about 210 million ha abandoned in 1990 (cf. Fig. 1 in Cramer et al., 2008)) is occurring mainly in Europe, North America and Oceania, with the most drastic decrease in agricultural lands (by about a third) seen in Europe (cf. Panel 1a in Queiroz et al., 2014). Land abandonment is a type of land use transformation that potentially causes the recovery of ecosystems (Cerdà et al., 2018). Passive revegetation in permanently abandoned arable land (called secondary succession) is characterized by the replacement of arable plant species by vegetation that disperse from surrounding habitats and will be subsequently established (Csecserits et al., 2011). Such secondary succession initially starts with annual or biannual plants, is then followed by perennial forbs, grasses and shrubs, and finally under usual Central European conditions ending up in a forest (climax stage).

Farmland abandonment represents a significant land use change from cropping to a complex of plant successions. Throughout most of Europe, vegetation on abandoned farmland has evolved into dense forest or shrub. The expansion of vegetation explains, in part, the perceived decline in water resources, reductions in soil loss and sediment delivery, and the progressive improvement of soil characteristics (García-Ruiz and Lana-Renault, 2011).

Vegetation change can also induce soil water repellency (SWR), which parameters are influenced by soil temperature (Novák et al., 2009), moisture (Leelamanie and Nishiwaki, 2019; Oostindie et al., 2017), texture (Benito et al., 2019), pH (Diehl et al., 2010), soil organic carbon (SOC) and clay (mainly kaolinite) content (Lichner et al., 2002). SWR may affect soil properties with depth (Orfánus et al., 2016; Sepehrnia et al., 2017) and time (Orfánus et al., 2014; Moret-Fernandez et al., 2019), and has positive effects on the stability of soil aggregates (Fér et al., 2016). Soil compaction may reduce SWR mainly as a consequence of decreased surface roughness (Bryant et al., 2007), but the hydrophobic conditions are readily restored a few days after removal of compaction load. Soil water repellency can be alleviated by addition of lime (Roper, 2005), kaolinite clay (Lichner et al., 2002; McKissock et al., 2000), and wax degrading bacteria (Roper, 2006). Naveed et al. (2019) found that the large impact of plant exudates and mucilages on water retention characteristics could be explained by differences in surface tension, contact angle and viscosity between exudates and mucilages of different origin. These properties may be driven by the relative amounts of organic acids and sugars (free and polysaccharide derived) in the exudates and mucilages. Guo et al. (2016) and Nik et al. (2015) also found the chemical composition of SOC changes during vegetation evolution.

Primary succession was found to increase SWR parameters and SOC content in acidic sandy soils in the Borská nížina lowland, Slovakia (Lichner et al., 2018), however there is a lack of knowledge in terms of secondary succession. The objective of this research was thus to estimate the effects of secondary succession during 28 years lasting abandonment of agricultural fields on chemical (pH and SOC content), hydrophysical (water sorptivity and hydraulic conductivity), and water repellency parameters (water drop penetration time, water repellency cessation time, repellency index, and modified repellency index),
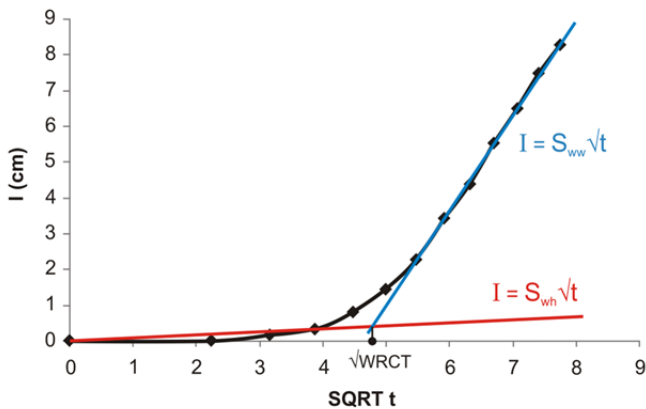
Fig. 1. The hockey-stick-like relationship of the cumulative infiltration of water (I) against the square root of time (SQRT t) for a sandy soil. The water sorptivity $S_{wh}(-2 \text{ cm})$ for water-repellent state of soil and the water sorptivity $S_{ww}(-2 \text{ cm})$ for nearly wettable state of soil were estimated, respectively, from the two different slopes of the relationship. The water repellency cessation time (WRCT) was estimated from the point of intersection of two straight lines, representing the $I = f(\text{SQRT } t)$ relationships for water-repellent and nearly wettable states of the soil.

as well as ethanol sorptivity of the top layer of three acidic sandy soils in the Borská nížina lowland, Slovakia. We hypothesize that the soil chemical and hydrophysical parameters will decrease, while the soil water repellency parameters will increase with the duration of abandonment.

MATERIAL AND METHODS
Study sites

The experimental sites S1, S2 are located at Sekule village (48°36′58.2′′ N, 16°59′39.0′′ E), while the experimental site S3 is placed at Studienka village (48°31′49.3′′ N, 17°08′34.5′′ E) in the Borská nížina lowland (southwestern Slovakia). The closest distance between the sites in Sekule and Studienka is about 12 km. According to the Köppen-Geiger climate classification, the region has temperate climate without dry season, warm summer (Cfb) (Kottek et al., 2006). Mean annual precipitation is about 550 mm, which is mainly summer-dominant. Elevation is 158 m a.s.l. at Sekule and 299 m a.s.l. at Studienka. Site S1 was a cultivated agricultural area planted with barley (*Hordeum vulgare* L.) in 2017. Site S2, abandoned for 12 years, is an early succession stage dominated by psammophilous grass *Corynephorus canescens* (L.) P. Beauv. with an admixture of other psammophytes and sand-tolerant weeds, such as *Bromus tectorum* L., *Cerastium semidecandrum* L., *Acetosella vulgaris* Fourr., *Anthemis ruthenica* M. Bieb., *Conyza canadensis* (L.) Cronquist, *Filago arvensis* L., *Myosotis stricta* Link ex Roem. et Schult., *Setaria pumila* (Poir.) Roem. et Schult., *Spergula morisonii* Boreau, *Trifolium arvense* L., *Veronica dillenii* Crantz, *Chondrilla juncea* L., and *Crepis* sp. Site S3 is a former arable land abandoned for 28 years. It is covered by synanthropized grassland dominated by *Festuca rupicola* Heuff. and *Chondrilla juncea* L., which are accompanied by admixture of psammophilous species (e.g. *Corynephorus canescens* (L.) P. Beauv., *Jasione montana* L., *Acetosella vulgaris* Fourr.) and sand-tolerant weeds (e. g. *Calamagrostis epigejos* (L.) Roth, *Setaria pumila* (Poir.) Roem. et Schult., *Conyza canadensis* (L.) Cronquist). The soils of the Sekule and Studienka sites are classified as Arenosol (WRB, 2014) and have sandy texture (Soil Survey Division Staff, 1993).

Methods
Laboratory methods

Basic soil properties were determined on disturbed samples with two replicates in the ISO Certified Laboratory of the Soil Science and Protection Research Institute in Bratislava. Particle size distribution was determined by sieving and sedimentation according to ISO 11277 (2009), pH(KCl) and pH(H$_2$0) were measured according to ISO 10390 (2005), SOC content was determined by oxidation with $K_2Cr_2O_7$-H_2SO_4 and titration of non-reduced dichromate according to ISO 10694 (1995), and carbonate content was determined from the volume of CO_2, produced during the decomposition of carbonates with about 10% hydrochloric acid, according to ISO 10693 (1995). The disturbed soil samples were taken randomly within an area of 25 m^2 in the surface (0–5 cm) layer at S1 site on 2 August 2018, at S2 site on 30–31 July 2018, and at S3 site on 9 October 2018.

Field methods

All the measurements of soil hydrophysical and SWR parameters were carried out on the surface of the studied soils during the hot and dry spell and the number of their replicates is presented in Table 2. The above-mentioned parameters were measured and the disturbed soil samples for laboratory determination of physical and chemical properties were taken from the top (0–5 cm) layer on 2 August 2018 (Site S1), 30–31 July 2018 (Site S2), and 9 October 2018 (Site S3). The places for the infiltration runs were chosen in the neighbourhood of each vegetal species and the surface to put the infiltrometers was flattened.

The volumetric water content, w (% vol), of the superficial (0–5 cm) soil layer was measured with a moisture meter type HH2 and soil moisture sensor SM200 (Delta-T Devices Ltd, Cambridge, UK).

Field water and ethanol infiltration measurements were performed with a minidisk infiltrometer (MDI) (Decagon, 2012) under a negative tension $h_0 = -2$ cm (Alagna et al. 2017, 2019). The cumulative infiltration I was calculated based on the Philip infiltration equation:

$$I = C_1 t^{1/2} + C_2 t + C_3 t^{3/2} + \ldots + C_m t^{m/2} + \ldots \tag{1}$$

where C_1, C_2, C_3, …, and C_m are coefficients, and t is time.

The sorptivity, $S(-2 \text{ cm})$, was estimated from the first term of the Philip infiltration equation ($I = C_1 t^{1/2}$) during early-time infiltration of water and ethanol (Clothier et al., 2000):

$$S(-2 \text{ cm}) = I / t^{0.5} \tag{2}$$

Duration of early-time infiltration is 60–180 s for a wettable (WDPT = 0–5 s) and slightly repellent (WDPT = 5–60 s) soil (Hallett, 2008), or it is equal to the time of passing the first five bubbles (with the total volume of about 1 mL) through MDI (Time to First Five Bubbles, TFFB, in Beatty and Smith, 2014) for strongly (WDPT = 60–600 s), severely (WDPT = 600–3600 s), and extremely (WDPT > 3600 s) water repellent soils. During this time the process is dominated by the capillarity and the other terms of the Philip infiltration equation can be neglected.

Equation (2) was used to calculate both the water sorptivity ($S_w(-2 \text{ cm})$) and ethanol sorptivity ($S_e(-2 \text{ cm})$) from the cumulative infiltration *vs.* time relationships taken from the MDI measurements. It was found that S_w is not function of water source tension, but is function of initial soil water content. The highest value of S_w corresponded to the lowest soil water con-

tent, remaining practically constant in a large range of soil water content, and abruptly decreasing near saturation toward zero (Villarreal et al., 2019). It should be mentioned that the water sorptivity depends on SWR and soil pore size, and ethanol sorptivity depends mainly on soil pore size.

The repellency index RI (Decagon, 2012; Hallett and Young, 1999; Lichner et al., 2007)

$$RI = 1.95 \, S_e(-2 \text{ cm}) / S_w(-2 \text{ cm}) \qquad (3)$$

was estimated from the combination of all the ethanol and water sorptivities, i.e., m × n values of RI were calculated from m values of $S_w(-2$ cm) and n values of $S_e(-2$ cm) (Pekárová et al., 2015). The RI values correlated closely with water drop penetration time (WDPT), which was used to develop a classification of RI by Iovino et al. (2018).

In the second method of estimating the RI, the water sorptivity $S_{wh}(-2$ cm) for water-repellent state of soil and the water sorptivity $S_{ww}(-2$ cm) for nearly wettable state of soil were estimated, respectively, from the slopes of the initial and subsequent stages of hockey-stick-like relationship (Fig. 1), and used to calculate a modified repellency index RI_m (Sepehrnia et al., 2016):

$$RI_m = S_{ww}(-2 \text{ cm}) / S_{wh}(-2 \text{ cm}) \qquad (4)$$

The persistence of SWR was assessed by both the WDPT and water repellency cessation time, WRCT (Lichner et al., 2013). The WDPT test involves placing a 50±5 μL water drop from a standard medicine dropper or pipette on the soil surface and recording the time of its complete penetration. A standard droplet release height of approximately 10 mm above the soil surface was used to minimize the cratering effect on the soil surface (Doerr, 1998; Tinebra et al., 2019). The following classes of the persistence of SWR were distinguished: wettable or non-water-repellent soil (WDPT < 5 s), slightly (WDPT = 5–60 s), strongly (WDPT = 60–600 s), severely (WDPT = 600–3600 s), and extremely (WDPT > 3600 s) water repellent soil (Bisdom et al., 1993). The values of WRCT were estimated from the intersection of two straight lines, representing the two stages of infiltration (Fig. 1).

Field water infiltration measurements with the MDI under a negative tension $h_0 = -2$ cm were used to estimate the hydraulic conductivity $k(-2$ cm). Zhang (1997) proposed to use the first two terms of the Philip infiltration equation to fit the cumulative infiltration vs. time relationship and estimate the hydraulic conductivity $k(-2$ cm) from equation:

$$k(-2 \text{ cm}) = C_2 / A \qquad (5)$$

where A is a dimensionless coefficient. Fitting of the two terms infiltration equation to cumulative infiltration data was performed through the linearization technique suggested by the Minidisk Infiltrometer User's Manual (Decagon, 2012). A value of $A = 1.73$, corresponding to sandy soil and suction $h_0 = -2$ cm, was used to calculate the hydraulic conductivity $k(-2$ cm). Given capillarity can be ignored at long times, estimation of k is expected to be more accurate as t increases (Zhang, 1997). The MDI experiments were therefore conducted until apparent steady state conditions were observed.

Statistical treatment

The statistical analysis to find differences between the parameters estimated in different sites was performed with NCSS 12 Statistical Software (2018), using single factor ANOVA and Tukey's Honestly Significant Difference (HSD) post-hoc test (p < 0.05). The Tukey-Kramer method (also known as Tukey's HSD (Honest Significant Difference) method) uses the Studentized Range distribution to compute the adjustment to c_α. The Tukey-Kramer method achieves the exact alpha level (and simultaneous confidence level $(1 - \alpha)$) if the group sample sizes are equal and is conservative if the sample sizes are unequal. The Tukey-Kramer test is one of the most powerful all-pairs testing procedures and is widely used.

The Tukey-Kramer adjusted critical value for tests and simultaneous confidence intervals is

$$c_\alpha = \frac{q_{1-\alpha,k,v}}{\sqrt{2}} \qquad (6)$$

where $q_{1-\alpha,k,v}$ is the $1 - \alpha$ quantile of the studentized range distribution.

RESULTS AND DISCUSSION

Basic soil-physical and chemical properties are presented in Table 1. A decrease in pH value of the studied soils from 6.55 to 4.50 was registered after 28-year lasting abandonment of agricultural fields in southwestern Slovakia. The great decrease in pH value in the studied abandoned fields is consistent with the findings of Zhao et al. (2014) during progressive succession of vegetation (grassland, shrubland, forest) occurring in karst sites in southwestern China, as well as Bautista-Cruz and del Castillo (2005) during the development of second-growth forest after abandonment of agricultural fields in tropical montane cloud forest areas in southern Mexico.

The significant decrease in pH value during abandonment was accompanied with the significant decrease in SOC content (Table 1) and significant increase in SWR parameters (Table 2), indicating that the composition of organic matter and its overall effectiveness to influence the wetting properties of soil particles is more important than the total amount of soil organic carbon (Ellerbrock et al., 2005). It should be mentioned that the SOC content in the top layer of acidic sandy soil under grass cover in Studienka is about 2-times less than the SOC content in the top layer of acidic silt loam soil under grass cover in Hněvčeves, the Czech Republic (0.80% vs. 1.74%) (Kodešová et al., 2011). Substantially higher clay and silt content in the top layer of Hněvčeves soil in comparison with that of Studienka soil (87.72% vs. 3.52%) resulted in better ability to accumulate organic matter.

Statistical characteristics of soil hydrophysical parameters $(k(-2$ cm) and $S_w(-2$ cm)), ethanol sorptivity, $S_e(-2$ cm), and soil water repellency parameters (WDPT, WRCT, RI, and RI_m) of the top layer of acidic sandy soils from the sites S1, S2 (Sekule, Slovakia), and S3 (Studienka, Slovakia) are presented in Table 2. As to the hydrophysical and chemical parameters, the mean value of $S_w(-2$ cm) decreased about 2.8 times, $k(-2$ cm) about 15.6 times, and SOC content about 2.3 times, while $S_e(-2$ cm) did not change significantly after 28 years lasting abandonment of agricultural field with acidic sandy soil in the Borská nížina lowland, Slovakia. As the ethanol sorptivity depends mainly on soil pore size, the last finding could mean that the soil pore size of acidic sandy soil did not change during succession. Soil structure is poorly developed in sandy soils whereas soil compaction due to human activity was negligible, thus pore size distribution is mainly determined by particle size distribution that is a relatively stable soil property at this time scale (Table 1). The results of $S_w(-2$ cm) (0.679±0.469 mm $s^{-1/2}$) and $k(-2$ cm) (9.1±7.5 μm s^{-1}) estimated in acidic

sandy soil at the 28 years abandoned agricultural field covered with grass created by secondary succession at Studienka are not significantly different from the results of S_w(–2 cm) (1.14±0.677 mm s$^{-1/2}$) and k(–2 cm) (48.0±35.0 µm s^{-1}) estimated in an acidic sandy soil under grass created by primary succession at Sekule (Šurda et al., 2015). It could mean that the values of hydraulic conductivity and water sorptivity of acidic sandy soil under grass do not depend on the type (primary or secondary) of succession resulting in the grass cover.

As to the soil water repellency parameters, the mean value of WDPT increased about 747 times, WRCT about 229 times, RI about 14 times, and RI$_m$ about 2.5 times after 28 years lasting abandonment of agricultural field with acidic sandy soil in the Borská nížina lowland, Slovakia. The increase in WDPT is consistent with the findings of Hewelke (2019) who registered an increase in WDPT after excluding albic Podzols from agricultural production. The results of WDPT (949±568 s) and RI (35.0±58.7) estimated in acidic sandy soil at the 28 years abandoned agricultural field covered with grass created by secondary succession at Studienka are, respectively, smaller

and higher than the results of WDPT (1723±1610 s) and RI (4.27±2.05) estimated in acidic sandy soil under grass created by primary succession at Sekule (Šurda et al., 2015).

Dependence of soil parameters on the duration of field abandonment for the southwestern Slovakia sites is presented on Fig. 2. It can be seen that pH, S_w(–2 cm), and k(–2 cm) decreased continuously, WDPT, WRCT, RI, and RI$_m$ increased continuously, while S_e(–2 cm) did not change significantly with the duration of field abandonment. A similar course of soil parameters was observed during the primary succession in acidic sandy soils in Sekule and Mehlinger Heide, Germany (Lichner et al., 2018). Rather than the continuous increase or decrease in soil parameters with duration of field abandonment, a "zigzag" pattern of all but one (S_e(–2 cm)) soil parameter relationships was registered during the 44 years lasting abandonment of agricultural field with alkaline sandy soils in Csólyospálos, Hungary (Lichner et al., 2018). This can be explained by the different vegetation cover and the resulting changes in the vegetation uptake of fertilizers and production of root exudates (cf. Naveed et al., 2019) and thatch.

Table 1. Physical and chemical properties of the top (0–5 cm) soils taken from the experimental sites S1, S2, and S3. The results are presented in the form: arithmetic mean ± standard deviation. (SOC – soil organic carbon).

Attribute	S1	S2	S3
Clay (%)	3.663 ± 0.936	2.126 ± 0.202	2.750 ± 0.607
Silt 1–10 µm (%)	5.232 ± 0.483	1.886 ± 0.226	0.100 ± 0.017
Silt 10–50 µm (%)	6.641 ± 0.934	1.605 ± 0.424	0.673 ± 0.085
Sand 50–250 µm (%)	25.952 ± 4.121	20.608 ± 3.511	26.607 ± 2.052
Sand 0.25–2 mm (%)	58.516 ± 6.479	73.775 ± 4.364	69.870 ± 2.761
CaCO$_3$ (%)	<0.05	0.10 ± 0.03	<0.05
SOC (%)	1.80[a] ± 0.11	1.06[b] ± 0.04	0.80[b] ± 0.06
pH (H$_2$O)	6.55[a] ± 0.06	5.60[b] ± 0.03	4.50[c] ± 0.03
pH (KCl)	6.25[a] ± 0.03	4.20[b] ± 0.03	4.16[b] ± 0.01

Properties denoted with different letters are significantly different on significance level 0.05.

Table 2. Statistical characteristics of soil hydrophysical parameters (namely the hydraulic conductivity, k(–2 cm), water sorptivity, S_w(–2 cm), and ethanol sorptivity, S_e(–2 cm)) and soil water repellency parameters (namely the water drop penetration time, WDPT, water repellency cessation time, WRCT, repellency index, RI, and modified repellency index, RI$_m$) of the top layer of acidic soils from the sites S1, S2, and S3.

Site	Attribute	Minimum	Maximum	Median	Mean	Standard deviation	Number of replicates
S1	w (% vol)	<0.1	<0.1	<0.1	<0.1	<0.1	10
	k(–2 cm) (µm s^{-1})	6.6	228	158	142[a]	66	10
	S_w(–2 cm) (mm s$^{-1/2}$)	1.31	2.42	1.94	1.89[a]	0.35	10
	S_e(–2 cm) (mm s$^{-1/2}$)	2.10	2.63	2.29	2.33[a]	0.25	4
	WDPT (s)	1	2	1	1.27[a]	0.47	11
	WRCT (s)	5.10	8.77	6.45	6.68[a]	1.45	10
	RI (–)	1.69	3.91	2.32	2.49[a]	0.57	40
	RI$_m$ (–)	2.54	5.91	5.19	4.59[a]	1.27	10
S2	w (% vol)	<0.1	<0.1	<0.1	<0.1	<0.1	10
	k(–2 cm) (µm s^{-1})	12.7	69.4	46.6	42.3[b]	24.4	10
	S_w(–2 cm) (mm s$^{-1/2}$)	0.42	1.48	1.08	1.03[b]	0.38	10
	S_e(–2 cm) (mm s$^{-1/2}$)	1.49	2.39	2.09	2.01[a]	0.40	4
	WDPT (s)	2	1520	20	179[a]	448	11
	WRCT (s)	8.8	99.6	33.4	36.5[a]	25.5	10
	RI (–)	2.0	11.1	3.64	4.59[a]	2.54	40
	RI$_m$ (–)	3.5	13.4	4.82	5.62[a,b]	2.96	10
S3	w (% vol)	<0.1	3.0	0.45	0.79	1.06	10
	k(–2 cm) (µm s^{-1})	0	19.7	9.0	9.1[b]	7.5	10
	S_w(–2 cm) (mm s$^{-1/2}$)	0.02	1.21	0.83	0.68[b]	0.47	10
	S_e(–2 cm) (mm s$^{-1/2}$)	1.93	2.39	2.01	2.08[a]	0.21	4
	WDPT (s)	20	1960	980	949[b]	568	15
	WRCT (s)	61.9	4172	1065	1572[b]	1463	9
	RI (–)	3.1	221	5.1	35.0[b]	58.7	40
	RI$_m$ (–)	3.6	30.8	6.6	11.4[b]	9.5	9

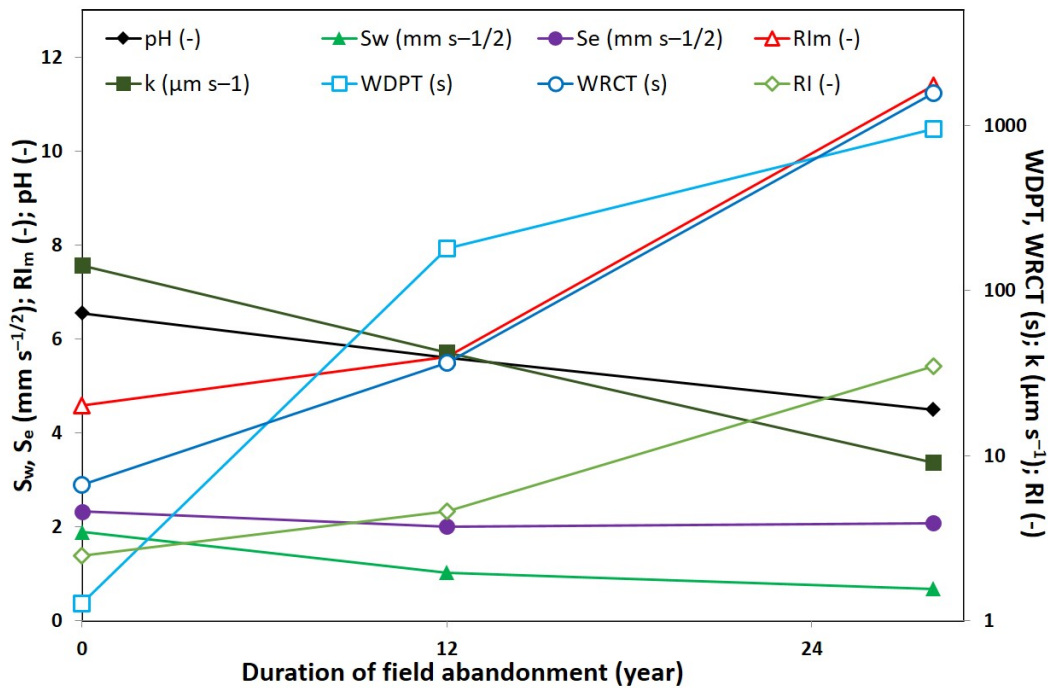Properties denoted with different letters are significantly different on significance level 0.05.

Fig. 2. Soil water repellency parameters (water drop penetration time, WDPT, water repellency cessation time, WRCT, repellency index, RI, and modified repellency index, RI_m) and soil hydrophysical parameters (hydraulic conductivity, $k(-2\ cm)$, water sorptivity, $S_w(-2\ cm)$, and ethanol sorptivity, $S_e(-2\ cm)$) of the top layer of acidic soils vs. duration of field abandonment relationships for the southwestern Slovakia sites.
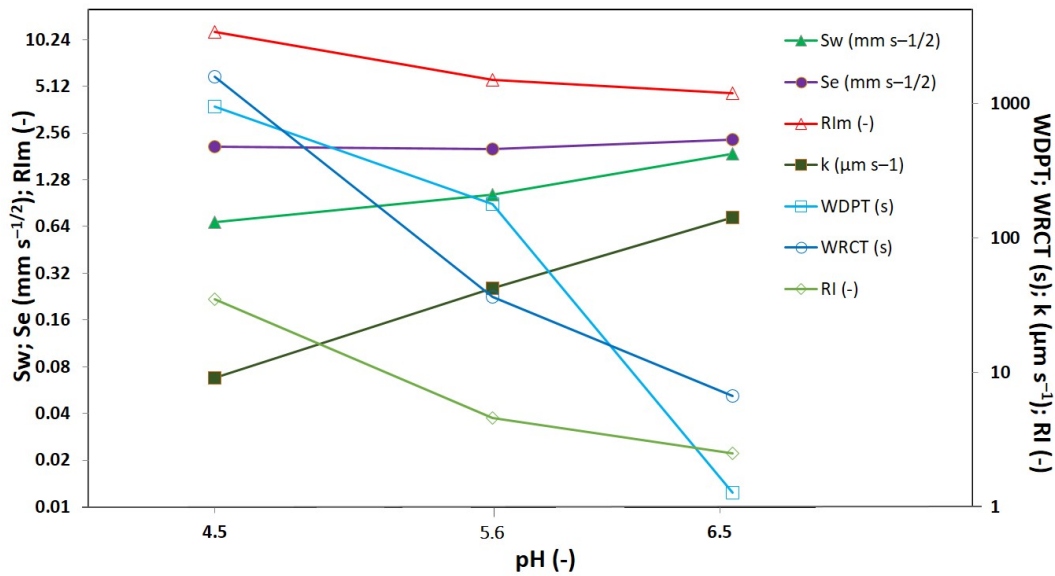

Fig. 3. Soil water repellency parameters (water drop penetration time, WDPT, water repellency cessation time, WRCT, repellency index, RI, and modified repellency index, RI_m) and soil hydrophysical parameters (hydraulic conductivity, $k(-2\ cm)$, water sorptivity, $S_w(-2\ cm)$, and ethanol sorptivity, $S_e(-2\ cm)$) of the top layer of acidic soils vs. pH relationships for the southwestern Slovakia sites.

Dependence of soil parameters on pH for the southwestern Slovakia sites is presented on Fig. 3. It can be seen that $S_w(-2\ cm)$, and $k(-2\ cm)$ increased continuously, WDPT, WRCT, RI, and RI_m decreased continuously, while $S_e(-2\ cm)$ did not change significantly with pH. The decrease in WDPT with an increase in pH value in the studied abandoned fields is consistent with the findings of Diehl et al. (2010).

CONCLUSION

Abandonment of agricultural fields with acidic sandy soil in the Borská nížina lowland, Slovakia, results in a significant decrease in the hydrophysical (water sorptivity and hydraulic conductivity) and chemical (pH and soil organic carbon content) parameters, significant increase in the water repellency

(water drop penetration time, water repellency cessation time, repellency index, and modified repellency index) parameters, but insignificant change in the ethanol sorptivity. As the ethanol sorptivity depends mainly on soil pore size, the last finding could mean that the soil pore size of acidic sandy soil did not change during succession.

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