



Application of electrical capacitance measurement for *in situ* monitoring of competitive interactions between maize and weed plants

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Abstract

Applicability of root electrical capacitance (EC) measurement for monitoring of crop–weed competition was studied in a pot experiment. Maize (*Zea mays* L.) was grown both alone and with *Echinochloa crus-galli* or *Abutilon theophrasti* in different densities with regular measurement of root EC. Plants were harvested 42 days after planting to determine above- and belowground biomass. Depending on weed density, *E. crus-galli*–*A. theophrasti* interaction reduced the root EC of maize by 22–66% and 3–57%, respectively. Competitive effect of crop on weeds and intraspecific competition among weeds could also be detected by EC values: *E. crus-galli* was less sensitive both to the presence of maize and to intraspecific competition than *A. theophrasti*. Strong linear correlations between root dry mass and root EC for crop and weeds (with R^2 from 0.901 to 0.956) were obtained by regression analyses at the end of the experiment. EC monitoring informed us on the emergence time of competition: *E. crus-galli* interfered with maize root growth a week earlier than *A. theophrasti*, and increasing weed densities accelerated the emergence of competition. In conclusion, the simple, non-destructive EC method should be considered a potential *in situ* technique for pot studies on crop–weed competition, which may partially substitute the intrusive techniques commonly used in agricultural researches.

Additional key words: *Abutilon theophrasti*; biomass loss; *Echinochloa crus-galli*; maize; root capacitance; root growth; weed competition.

Abbreviations used: DAP (day after planting); EC (root electrical capacitance); Φ (phase angle).

Authors' contributions: Designed and set up the experiment, accomplished the electrical measurements, participated in plant harvest, wrote the publication: IC. Gave help in plant cultivation and data interpretation, improved the publication scientifically: TT. Carried out the plant harvest, biomass determination and statistical analysis: AF and KRV. Supervised the work and coordinated the research project: EL.

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Introduction

Excluding environmental variables, weed competition is the major constraint to crop production for many agroecosystems worldwide. Besides serious yield losses, various damages including the increased cost of cultivation, reduced quality of field products, propagation of pests and diseases, secretion of phytotoxins or reduced irrigation efficiency may be attributed to weed infestation (Holm *et al.*, 1991). Investigation of the mechanisms and outcomes of crop–weed competi-

tive interactions becomes increasingly important for designing more efficient and economical weed management strategies in agricultural areas (Craine & Dybzinski, 2013; Lehoczky *et al.*, 2013). Most studies tend to focus only on the aboveground symptoms of plant interference, even if roots play a key role in competition for place, water, and nutrients (Rajcan & Swanton, 2001; Trinder *et al.*, 2013). The insufficient information on belowground phenomena can be obviously attributed to the hidden character of plant roots associated with the cumbersome root sampling procedures.

Measurement of electrical capacitance (EC) in a plant–soil system is capable to provide a rapid assessment about the extension of root systems without damaging plants. The method was developed by Chloupek (1972) using numerous crop species under greenhouse and field conditions. By applying a capacitance meter (LCR-instrument) with alternating current, EC can be measured between a ground electrode embedded in the soil and a plant electrode fixed on the plant stem. The magnitude of EC proved to be positively correlated with root weight, root surface area or root length. First Dalton (1995) presented a conceptual model for describing the plant root–soil system in which root surface area was considered to be the surface area of a group of circular cylinders having the same average diameter as the cellular system constituting the roots (Fig. S1 [suppl.]). According to the root–soil–electrode network model, xylem and phloem sap in plant roots forms a low-resistance electrical conduit which is separated from a low-resistance external soil or nutrient solution by insulating root membranes. The capacitance of this root–soil interface is proportional to the charge accumulated on the membrane surfaces; thus the membrane polarized by an alternating current plays the role of a dielectric in a capacitor.

The EC can be specified by its magnitude and phase angle (Φ , in degrees); the latter shows the phase difference between current and voltage, indicating the “capacitive strength” as a tendency of plant root to behave as a capacitor. The root–soil system is a relatively poor capacitor. The phase angle is -90° in ideal capacitors irrespective of current frequency, but in the root–soil systems, Φ is much lower in general; furthermore, it depends on the applied current frequency and also on soil properties and plant age (Aubrecht *et al.*, 2006; Cseresnyés *et al.*, 2013a). Phase angle is the dielectric component of the plasma membrane, and is basically determined by the physicochemical structure of the root tissue. Though Φ in itself does not indicate root extension and activity, its magnitude and temporal changes can inform us on the age-dependent alteration of root structure and functionality.

The main limitation of the EC method is the sensitivity of electrical properties to soil water saturation, ionic status, soil texture and to the distance of plant electrode from substrate surface (Ozier-Lafontaine & Bajazet, 2005; Dietrich *et al.*, 2012). Nevertheless, under well-defined conditions (constant soil moisture content, soil salinity and consistent electrode placement) and by the application of an effective current frequency, the method can provide a good estimation of the root system size. On the one hand, the technique can be used for relative comparison of root development; on the other, it is possible to formulate calibration relationship

with reasonable predictive ability to assess the root properties for a given plant in a given soil (McBride *et al.*, 2008). Reliability of the technique has been demonstrated by various pot experiments and field studies focused on crop plant genotypes (Beem *et al.*, 1998; Svačina *et al.*, 2014; Heřmanská *et al.*, 2015) and young tree cultivars (Preston *et al.*, 2004; Cao *et al.*, 2010; Pitre *et al.*, 2010) in most cases. The great advantage of EC method over other *in situ* techniques that it can simply study the functional aspect of the plant root system, providing information about the absorptive root surface area (Cseresnyés *et al.*, 2013b).

The aim of this methodological work presented was to test the applicability of EC measurement for *in situ* monitoring of root development and biomass loss of crop and weed plants subjected to competitive interactions in a pot experiment with two weeds native to southern Asia which (due to their broad ecological adaptation) have become widely distributed in various agricultural areas of the Northern Hemisphere during the last century. They are considered to be among the most troublesome yield-limiting weeds in many temperate and tropical crops including maize, rice, cotton, sorghum, soybean, cassava and vegetables (Warwick & Black, 1988; Holm *et al.*, 1991; Hyvönen & Ramula, 2014).

Material and methods

Plant species

Our study focused on interactions between maize (*Zea mays* L. cv. DC 488 F1) and *Echinochloa crus-galli* (L.) Beauv. (barnyardgrass) and *Abutilon theophrasti* Medic. (velvetleaf) weed species. A weed-free maize control (Z-0; one plant per pot) was compared with weed treatments at low, medium and high densities *i.e.* 1, 3 and 5 plants per pot, respectively, for studying the density-dependent competitive effect of weed on crop (the two weed species were not combined). The same densities of weeds were also set in pots free of maize in order to investigate the intraspecific weed interaction and to serve as controls for studying the effect of crop on weeds at different densities. Experimental treatments are listed in Table 1. They were replicated ten times.

Plant cultivation

Echinochloa crus-galli and *A. theophrasti* seeds were collected from natural weed populations developed on maize fields in Western Hungary. Maize and weed seeds were pre-germinated by placing them on moistened paper towel in Petri dishes and keeping at

Table 1. Overview of the experimental design with number of maize (*Zea mays*) and weed (*Echinochloa crus-galli*, *Abutilon theophrasti*) plants grown in pots

Treatment label	<i>Z. mays</i>	<i>E. crus-galli</i>	<i>A. theophrasti</i>
Z-0	1	–	–
Z-E1	1	1 (low)	–
Z-E3	1	3 (medium)	–
Z-E5	1	5 (high)	–
E1	–	1 (low)	–
E3	–	3 (medium)	–
E5	–	5 (high)	–
Z-A1	1	–	1 (low)
Z-A3	1	–	3 (medium)
Z-A5	1	–	5 (high)
A1	–	–	1 (low)
A3	–	–	3 (medium)
A5	–	–	5 (high)

26 °C for 2–5 days in darkness. Germination time was set to obtain a synchronous seedling emergence for each species. Seedlings were transplanted into plastic pots (17 cm in height and 15 cm in diameter at top) containing 3.8 kg of air-dried Arenosol (FAO-UNESCO, 80.9% sand, 11.9% silt and 7.2% clay) with $\text{pH}_{\text{H}_2\text{O}}$ of 7.52, cation exchange capacity of 8.39 mmol/100 g, 0.29% lime content, 1.20% humus content, 1.55 kg/L bulk density and 0.19 cm^3/cm^3 water content at field capacity. Total organic and mineral N content in soil was 730 mg/kg, ammonium-lactate-acetate extractable P and K were 438 and 222 mg/kg, respectively. A few more seedlings over the number of plants desired were deposited in each pot. Three days after planting (DAP), the surplus plants were removed for obtaining the required densities in all pots. Plants were grown in a growth chamber at 28/18 °C and 16/8 h for day/night temperature and photoperiod, respectively, and air humidity of 50–80%. A relatively low irradiance of 300 $\mu\text{mol}/\text{m}^2\cdot\text{s}$ produced by metal halide lamps was applied to ensure the possibility of light competition in the medium- and high-density weed treatments. Pots were arranged randomly with changing their places daily to avoid position effect. Planting medium in all pots was daily irrigated with tap water to field capacity: pots were placed on a balance (± 1 g) to water to a gross weight calculated from the soil volume and its water content at field capacity (0.19 cm^3/cm^3). The volumetric water content was measured with a TDR instrument (Trime FM3) then it was adjusted precisely to field capacity. A six-week (42 DAP) duration of experiment since sowing was chosen, firstly because the reliability of EC method is the greatest during the early vegetative stage of plant ontogeny (Cseresnyés *et al.*, 2013a; Ellis *et al.*, 2013b). Secondly, this time practically

covers the critical period of maize while crop is the most vulnerable to weed competition (Rajcan & Swanton, 2001).

Electrical measurements and biomass determination

EC and phase angle (Φ) were measured with a GW-8101G precision capacitance meter (GW Instek Co., Ltd., Taiwan) at 1000 Hz frequency with 1 V terminal voltage. One terminal of the instrument was connected to a stainless steel rod (6.3 mm in diameter and 15 cm long) inserted to a depth of 10 cm into the soil. The second terminal was attached to the plant stem with a spring tension clamp. Since the position of the stem electrode affects the electrical measurement, a distance of 15 mm was precisely maintained between the lower edge of the clamp and the soil surface. Electrocardiograph paste was smeared around the stem to keep up electric connection (Rajkai *et al.*, 2005). Two hours before the measurement the pots were brought into the laboratory (24 °C) and irrigated to field capacity (see above). In this manner, for every measuring date, soil moisture as measured by the TDR (time domain reflectometry) instrument was not significantly different among the treatments. Electrical measurements were carried out on ten occasions from 9 to 42 DAP. Weeds were measured only seven times from 20 DAP onwards, because of problems in electrode fastening to thin plant stem earlier.

At the end of the experiment, all plants were harvested; plant shoots were cut off and root systems were washed thoroughly off the soil. The mixture of intact root systems of each plant grown in common pot were immersed into a 12 L water-filled container, and carefully separated. Harvested shoots and roots were oven-dried at 70 °C for 72 h to determine dry biomass for each individual maize ($n=70$), *E. crus-galli* ($n=180$) and *A. theophrasti* ($n=180$) plants. For the 3 or 5 weeds grown in a common pot, an average root and shoot dry mass was calculated and used in ANOVA analysis.

Statistical methods

Statistical evaluation was performed by using the Statistica software (vers. 12, StatSoft Inc., OK, USA). The normality of each data group was checked by Kolmogorov–Smirnov test. Unpaired t-test or one-way ANOVA with Tukey–Kramer post-hoc test was used to compare means of data groups for EC, phase angle,

root and shoot dry mass and root/shoot ratio. In case that standard deviations of the compared groups were significantly different (shown by F-test or Bartlett test), Welch's corrected t-test or nonparametric Kruskal–Wallis test with Dunn post-hoc test was applied. Statistical significance was assessed at $p < 0.05$ in each case. The relationship between root EC and root dry mass measured at the end of the experiment for each species were evaluated by simple regression analysis ($p < 0.05$). Analysis of covariance was used to test for homogeneity of slopes.

Results

Electrical capacitance (EC)

In all treatments, root EC in maize increased over time till 27–31 DAP then decreased continuously. *Echinochloa crus-galli* competition treatments proved to clearly affect values of root EC in maize (Fig. 1A). EC detected for 42 DAP decreased with increases in weed density (by 22%, 43% and 66% with 1, 3 and 5 weeds per pot, respectively). Higher densities of *E. crus-galli* corresponded to an earlier effect of competition: signal intensity in root EC for Z-E1, Z-E3 and Z-E5 groups became significantly lower on 20, 16 and 13 DAP, respectively than those of maize control (Z-0). Intraspecific competition among weeds was also revealed by the EC method, as the increasing *E. crus-galli* density resulted in a significant decrease in root EC at each measurement time (Fig. 1B). At low and medium weed density, the presence of maize was observed to reduce root EC of *E. crus-galli*, which was significantly lower in Z-E1 and Z-E3 groups than in E1 and E3 plants, respectively. This crop interference was untraceable at high weed density (Z-E5 and E5). Phase angle (Φ) in maize increased till 27 DAP, thenceforward it declined continuously (Fig 1C); (since a higher negative Φ value indicates a higher phase angle in capacitors, Φ graphs are shown with inverted vertical axis). Viewing the last measurement (42 DAP), Φ decreased as weed density increased, however the difference was statistically significant only when Z-E5 group was compared with weed-free maize (Z-0). Phase angle measurement in *E. crus-galli* produced a similar concave curve with an apex on 31 DAP, but without significant differences among treatments (data not shown).

Density-dependent negative effect of *A. theophrasti* on maize EC readings is shown in Fig. 1D. Root EC in maize subjected to *A. theophrasti* competition was higher at any weed density than in maize with comparable densities of *E. crus-galli*. Compared to Z-0,

just a statistically non-significant (3%) reduction in maize EC was detected at low *A. theophrasti* density (Z-A1) at the last measurement, while 34% rate of decrease in EC was calculated at medium (Z-A3) and 57% at high (Z-A5) weed density. Weed competition effects on EC became significant ($p < 0.05$) from 23 and 16 DAP at medium and high weed density, respectively. Strong intraspecific competition occurred among *A. theophrasti* plants: increasing weed density resulted in a significant ($p < 0.05$) decrease of root EC at any measurement time (Fig. 1E). Rate of decrease in EC in relation to control *A. theophrasti* (A1) were higher both for A3 and A5 plants than was found for *E. crus-galli* in the same comparison. *Abutilon theophrasti* grown with maize showed significantly lower EC than did their crop-free counterparts irrespective of density. The phase angle graph of maize grown with *A. theophrasti* (Fig. 1F) was of similar shape to the graph obtained for maize–*E. crus-galli* competition. At the last measurement, Φ decreased as *A. theophrasti* density increased, but the difference was statistically significant only between Z-0 and Z-A5 treatments. No significant differences in Φ were found between *A. theophrasti* treatments (data not shown).

Plant biomass

Above- and belowground dry biomass obtained by plant harvest are reported in Figs. 2 and 3. Both the root and the shoot dry mass of maize declined significantly with increases in *E. crus-galli* density (Figs. 2A and 2B), while no significant change was detected in root/shoot ratio (Fig. 2C). Intraspecific competition reduced the root and shoot dry mass of *E. crus-galli* (Figs. 2D and 2E) without inducing alteration in root/shoot ratio (Fig. 2F). Under crop interference, root and shoot dry mass of weed decreased in the low- and medium-density treatment (Z-E1 and Z-E3) with unchanged root/shoot ratio, but biomass loss provoked by maize competition was insignificant for the high-density weed application (Z-E5).

Abutilon theophrasti grown with maize at low density (Z-A1) had no influence on root dry mass (Fig. 3A), shoot dry mass (Fig. 3B) and root/shoot ratio (Fig. 3C) of crop, confirming the EC measurement in this case, too. When medium (Z-A3) and high (Z-A5) weed density was applied, both the root dry mass and even more the shoot dry mass of maize decreased, leading to a significant increase in root/shoot ratio (by 15% and 23% for Z-A3 and Z-A5 groups, respectively). Intraspecific competition among *A. theophrasti* caused significant reduction

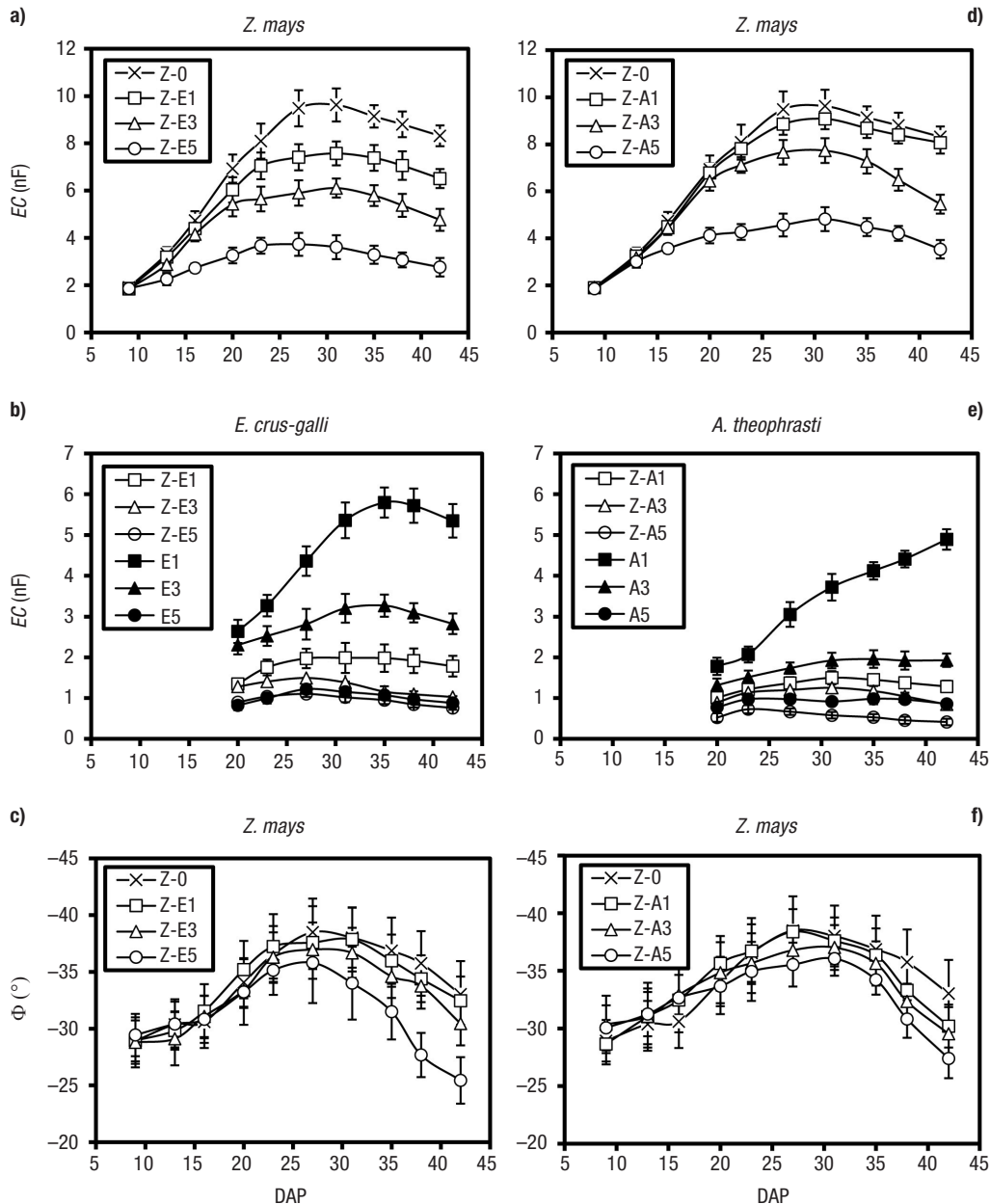


Figure 1. Signal intensity in root electrical capacitance (EC) related to time (DAP: day after planting) in *Zea mays* (A, D), *Echinochloa crus-galli* (B) and *Abutilon theophrasti* (E) plants. Temporal changes in phase angle (Φ) measured at *Z. mays* during the competition (C, F). See Table 1 for treatment labels.

in root and shoot dry mass (Figs. 3D and 3E) but did not alter the root/shoot ratio (Fig. 3F). Maize also impeded the weed growth; the competitive effect was stronger on shoot development than on root extension. Consequently, the root/shoot ratio of *A. theophrasti* increased significantly and the rate of change was inversely proportional to the density (106%, 60% and 26% for the low, medium and high weed density, respectively).

At the end of the experiment, we investigated how the relative decline in root EC in relation to maize (Z-0) or weed (E1 or A1) control indicates the relative bio-

mass loss of species subjected to inter- or intraspecific competition. As for maize competition either with *E. crus-galli* (Fig. 4A) or with *A. theophrasti* (Fig. 4B), the rate of decrease in root EC (42 DAP) compared with weed-free maize (Z-0) tended to consistently a bit lower than the loss of root dry mass and total dry biomass (but there were no statistical comparison). A similar comparison for *E. crus-galli* and *A. theophrasti* grown without (E3, E5, and A3, A5) or with maize (Z-E1, Z-E3, Z-E5, and Z-A1, Z-A3, Z-A5) in various densities, shows similar results in terms of EC values and biomass data (Figs. 4C and 4D).

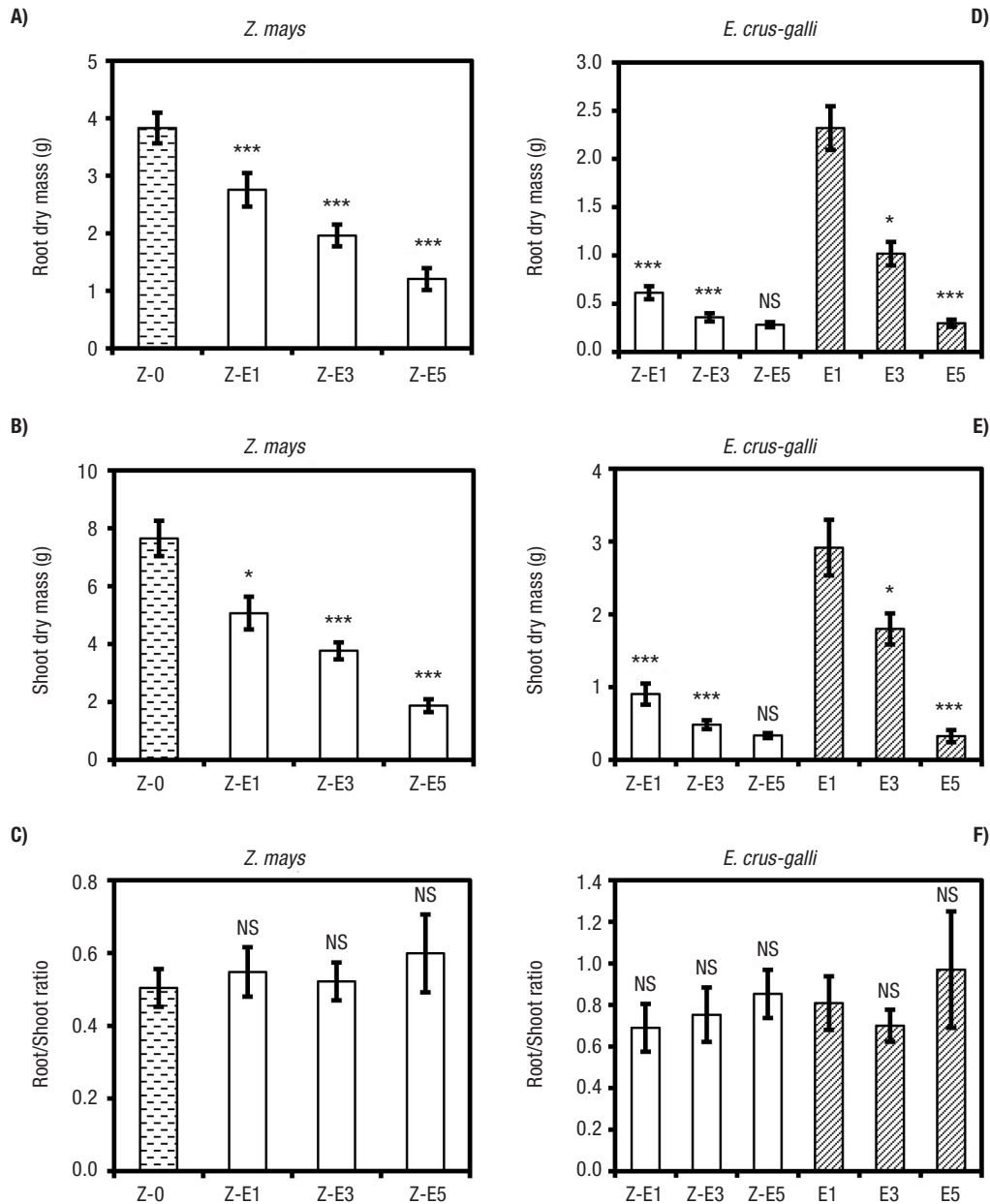


Figure 2. Root and shoot dry mass (g/plant) and root/shoot ratio of *Zea mays* (A, B, C) and *Echinochloa crus-galli* (D, E, F) plants at the end of the experiment. Means and standard deviations were calculated using the data of all plants involved in experiment. Asterisks show the significance levels (***, *, NS: $p < 0.001$, 0.05, non-significant, respectively) as follows: at *Z. mays* they indicate the differences from 'Z-0' (effect of weed on crop); at *E. crus-galli*, levels above 'Z-E1', 'Z-E3', 'Z-E5' bars mark the differences from 'E1', 'E3', 'E5' groups, respectively (effect of crop on weed); and above 'E3' and 'E5' bars mark the differences from 'E1' group (intraspecific competition among weeds). See Table 1 for treatment labels.

The regression analysis of root EC (42 DAP) of individual plants and root dry mass indicated strong linear correlation ($p < 0.001$) with $R^2 = 0.901$, 0.956 and 0.954 for maize, *E. crus-galli* and *A. theophrasti*, respectively (Fig. 5). Differences in slopes of regression lines were not statistically significant in the case of maize and *E. crus-galli* ($F_{1,126} = 4.5$, NS), whereas the regression line of *A. theophrasti* was significantly

steeper than that of maize ($F_{1,126} = 179$, $p < 0.01$) and *E. crus-galli* ($F_{1,126} = 336$, $p < 0.01$).

Discussion

The results show the ability of electrical capacitance measurement to investigate root mass *in situ* and to

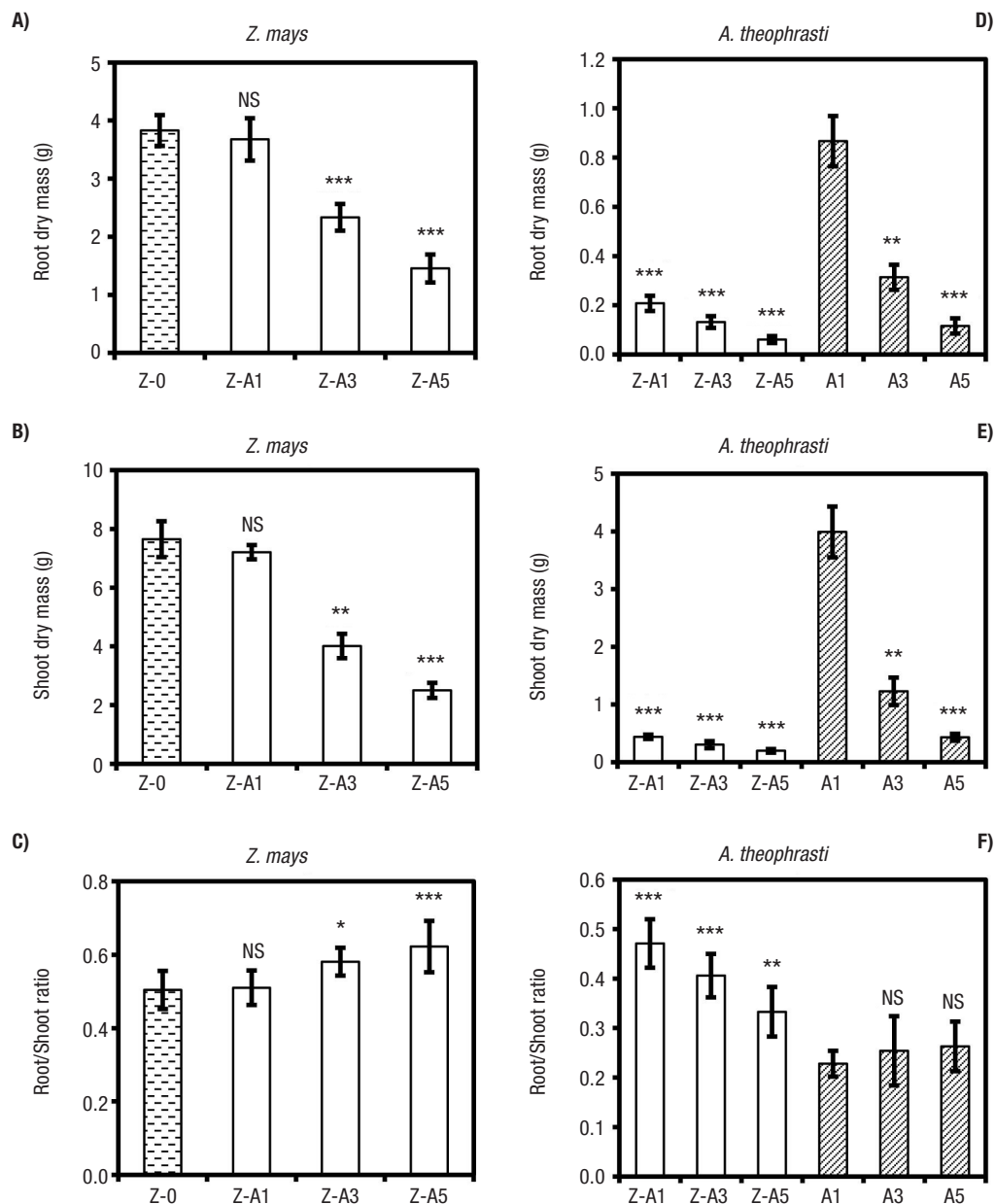


Figure 3. Root and shoot dry mass (g/plant) and root/shoot ratio of *Zea mays* (A, B, C) and *Abutilon theophrasti* (D, E, F) plants at the end of the experiment. Means and standard deviations were calculated using the data of all plants involved in experiment. Asterisks show the significance levels (***, **, *, NS: $p < 0.001$, 0.01, 0.05, non-significant, respectively) according to the order described at Fig. 2. See Table 1 for treatment labels.

show changes over time in relation to various competitive interferences. The rate of decrease in root EC caused by plant interaction is therefore a promising estimator for the strength and time-course of competition through the indication of the loss of above- and belowground biomass. In this respect, results obtained fit in with differences in competitive strategies evolved by the two weed species as reported in the literature: *Echinochloa crus-galli* is known to be an aggressive belowground competitor even in the early growth stage (Martinková & Honěk, 1998; Bajwa *et al.*, 2015). Its

fibrous root system overlays the crop roots quickly, resulting in effective water and nutrient extraction from the soil (Perera *et al.*, 1992; Chauhan & Abugho, 2013). Growth inhibition in crops is not only due to the decreased water and nutrient content, but rather to the reduced ability of crop roots to extend and reach resources (the phenomena is undoubtedly intensified by space limitation in pots). In our experiment, common nutrient and light deficiency symptoms, including thin stem, general chlorosis and enhanced senescence in older leaves of maize plants became visible first on

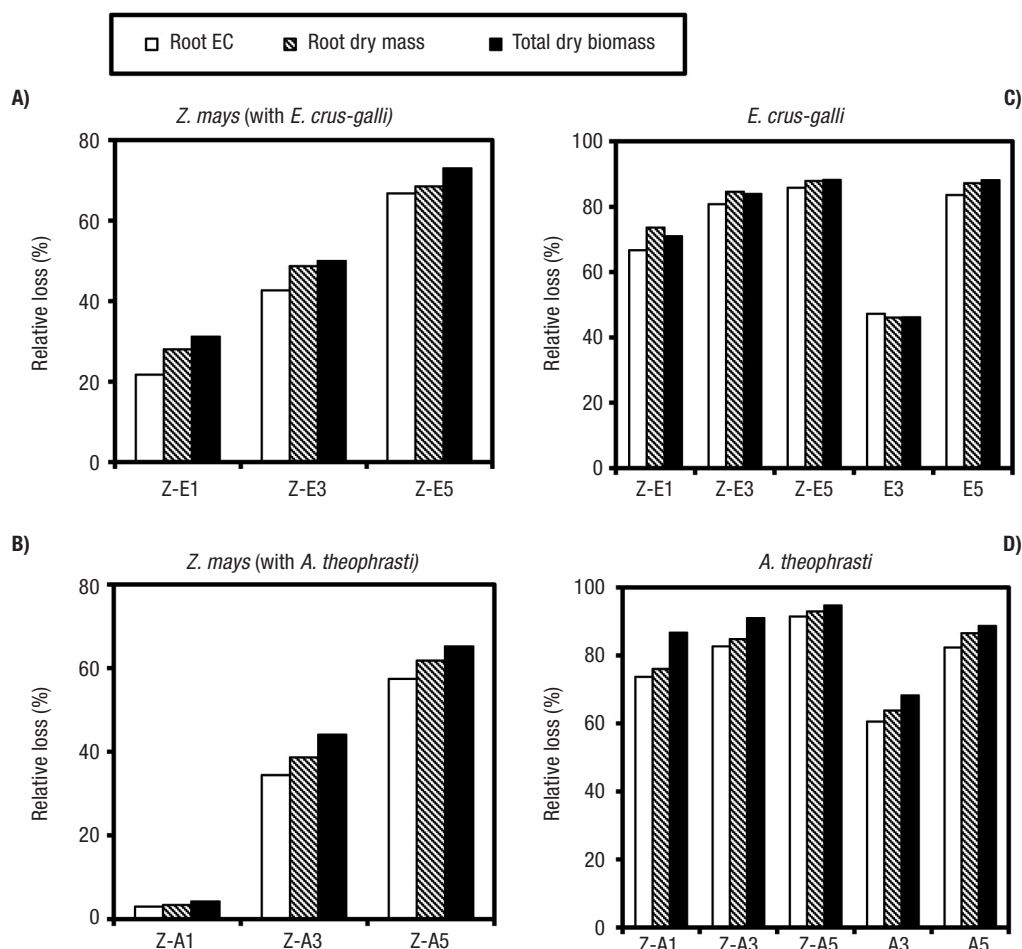


Figure 4. Relative loss (%) in root electrical capacitance (EC – measured on DAP 42), root dry mass and total dry biomass in *Zea mays* (A, B), *Echinochloa crus-galli* (C) and *Abutilon theophrasti* (D) caused by competition. At *Z. mays*, *E. crus-galli* and *A. theophrasti* plants, 100% are represented by the values of ‘Z-0’, ‘E1’ and ‘A1’ groups, respectively. See Table 1 for treatment labels.

16 and 20 DAP in Z-E5 and Z-E3 groups, respectively (5 and 8 days earlier than in the maize–*A. theophrasti* competition). The EC and biomass data supported concurrently the higher competitive capacity of *E. crus-galli* over crop in comparison with the impact of *A. theophrasti*, especially when weeds were grown with maize in low density (Fig. 4A and 4B). *Echinochloa crus-galli* proved to be less sensitive to intraspecific competition at medium density (E3) than *A. theophrasti*, and maize competitiveness was weaker over *E. crus-galli* than against *A. theophrasti* (Figs. 4C and 4D).

Abutilon theophrasti shows its competitive ability during the mid and late vegetative phase until the beginning of flowering (Sattin *et al.*, 1992; Nagy *et al.*, 2014). Weed causes maize yield loss principally through competition for light by overtopping the crop, and by producing allelopathic chemicals (Kazinczi *et al.*, 2001; Traore *et al.*, 2002; Bonifas & Lindquist, 2006). The outcome of maize–*A. theophrasti* competition can be determined

by water and nutrient (mostly the nitrogen) availability and by the relative emergence time of weed and crop (Lindquist *et al.*, 2007; Qaderi *et al.*, 2015). In our study, the optimal water and the limited nitrogen supply with the simultaneous maize–weed emergence did not allow *A. theophrasti* the rapid early growth and crop overtopping by the end of experiment. Thus, the decrease in root EC (likely inhibition in maize root growth) was detected later and only at high (Z-A5) and medium (Z-A3) weed density with the appearance of nutrient deficiency symptoms from 21 and 28 DAP in these groups, respectively. *Abutilon theophrasti* proved to be more sensitive both to intraspecific competition and to maize interference than *E. crus-galli*. When *A. theophrasti* grew without crop, partitioned proportionally more biomass to shoot versus root, irrespective of density. Competitive interaction with maize inhibited mainly the shoot development of weed, leading to a significant increase in root/shoot ratio.

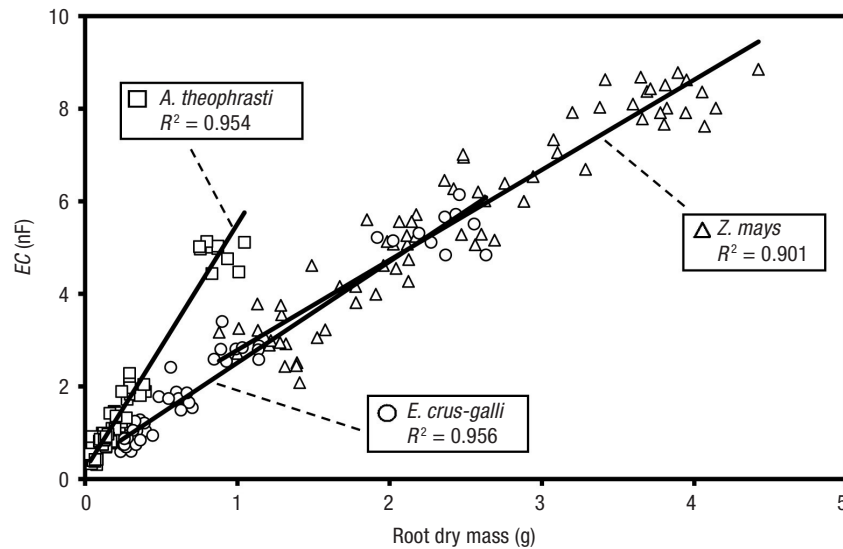


Figure 5. Relation of root electrical capacitance (EC – measured on DAP 42) with root dry mass (RDM) at *Zea mays* ($EC = 1.95RDM + 0.81$), *Echinochloa crus-galli* ($EC = 2.18RDM + 0.42$) and *Abutilon theophrasti* ($EC = 5.31RDM + 0.30$) plants. Each regression is significant at $p < 0.001$ level.

Temporal changes in the magnitude and phase angle (Φ) of EC in maize refer to the altering functionality and physicochemical structure of the root system (Rajkai *et al.*, 2005; Cseresnyés *et al.*, 2013a). Both parameters increased continually to a maximum, thereafter showed a downward trend (Fig. 1). The decrease is thought to be caused by root death and by the reduction in root activity due the deposition of the impermeable, electrically insulating suberin in endodermal cell walls (Dalton, 1995; Čermák *et al.*, 2006). The increasing weed competition (density) provoked an additional decrease in the Φ of maize root. The rising interference of weed roots is a strengthening constraint to crop root extension and proliferation that leads to an increasing proportion of older root segments to the younger ones. Therefore, the enhanced integrated root system age associated with the higher ratio of suberized root segments decreased the uptake activity (EC) and the capacitive strength (Φ) of the whole root system (Gao *et al.*, 1998). Since Φ is less sensitive to the altered root growth than the magnitude of EC, the change was significant solely at high weed densities (Z-E5 and Z-A5).

Regression analyses (Fig. 5) proved the feasibility of EC measurement for the accurate determination of root dry mass for each plant species applied. Considering EC a reliable indicator to active root surface and water uptake rate (Aubrecht *et al.*, 2006), it points to the plant specific differences in our case. Monocotyledonous maize and *E. crus-galli* seemed to maintain similar root uptake rate per root mass (nearly overlapping regression lines). The steeper regression line achieved for *A. theophrasti* refers to the higher root

uptake rate, which may be linked to a higher partitioning of biomass to shoot, leading in turn to a higher transpiration activity (particularly without competition effect). The positive intercept for the regressions is due to the electrode polarization (may occur up to a few kilohertz) and to the EC of plant stem between the soil surface and plant electrode (Ozier-Lafontaine & Bajazet, 2005). This is why the rate of decrease in root EC is consistently lower by a few percent than the relative biomass loss in the same comparison (Fig. 4). Nevertheless, the relative decline of root EC caused by competition seems to be a quite good indicator of the biomass loss. Though there was only one harvest at the end of this experiment, we formerly verified the close correlation between root biomass and EC in maize of different ages grown under different conditions by repeated plant harvest (Cseresnyés *et al.*, 2013b).

Our results illustrate that EC measurement in a plant–soil system is a promising and useful method for studying *in situ* the effect of competitive interferences on root extension, root function and on rate of change in biomass loss. The instrumental process is very simple, inexpensive, time-saving and principally non-destructive, thus is suited for continuous plant monitoring, approaching to the functional side of root development. By applying the EC method, not only the final outcome of plant interactions can be detected, but it is possible to obtain information about how the competitive growth inhibition be realized in time (decrease in root EC became significant 3–5 days before the appearance of nutrient deficiency symptoms). Competition experiments with EC measurements can be carried out by

growing various crop cultivars under different environmental variables (*e.g.* water regime, nutrient supply, temperature, light conditions, elevated CO₂ concentration, herbicide treatment) in order to study the effect of these factors on plant competitiveness. Nevertheless, it is important to emphasize, that measurement data are comparable only among plants of the same species, grown in the same substrate at the same moisture level in the same time frame (Chloupek *et al.*, 2010). A drawback to the method against conventional procedures (*i.e.* core sampling or rhizotrones) that EC does not provide information about the relative depth distribution and morphology of the roots, which plays important role in competition.

Though several studies demonstrate the relevance of the process in the field (Beem *et al.*, 1998; Preston *et al.*, 2004; Chloupek *et al.*, 2006; Ellis *et al.*, 2013b; Svačina *et al.*, 2014; Nakhforoosh *et al.*, 2014), EC method seemed to be reliable under relatively homogeneous soil conditions (*e.g.* sandy soils) with adequate water supply. Temporal changes in soil water content usually preclude the possibility of the continuous monitoring of root activity under real field conditions. In these cases, different treatments can be compared by using their single-time root EC data collected within one day without rain (Chloupek *et al.*, 2006, 2010), provided that soil water contents were statistically equal around all plant roots studied. It is advised to complete EC measurement simultaneously with the detection of soil moisture content (with a TDR instrument) in the root zone. If the investigation is carried out on a relatively large area, a systematic soil sampling (for assessing ionic status, texture and organic matter content) would be needed. Future experiments are worth completing with intermediate biomass sampling or with surveys focused on the relation of EC to soil texture or moisture. Variability of soil temperature may also affect the measured data. Field conditions are expected to require a higher number of replicates to cover the greater heterogeneity of plant population. Due to the limitations described above, the capacitance method is therefore appropriate for pot experiments carried out in growth chambers, greenhouses and outdoor with somewhat controlled external factors.

The EC measurement may be of interest for future applications, particularly in pot experiments. It can partially substitute or integrate the intrusive and time-consuming techniques commonly used or may be combined with other physiological investigation methods. The root system EC can become an important part of the biochemical or genetic data set for plant stress physiology researches (though it cannot be used for continuous drought stress as measurements are dependent on soil moisture). These functional approaches will be helpful

to understand and elucidate weed life strategies and competitive mechanisms for limiting resources in relation to both intra- and interspecific interactions.

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