ECOLOGICAL SIGNIFICANCE OF ASSIMILATE DISTRIBUTION IN *AGROPYRON REPENS* CLONES UNDER INFLUENCE OF THE COPPER SMELTER LEGNICA

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ABSTRACT

The studies on couch grass (*Agropyron repens* (L.) P. Beauv.) populations growing in stress conditions in close vicinity of a copper smelter concern the integrity of clonal structure. The connections of tillers within a clone and the interclonal integrity was investigated by means of assimilate translocation, using ^{14}C. It was found that heavy metal stress affects the phenotypic plasticity of couch grass in regard to clonal growth of the phalanx type. The phalanx type growth is supported by a considerable integration, which allows the redistribution of resources, through internal routes, from places rich in resources to such clone parts, which cover a surface poor in nutritive compounds. In an unpolluted (control) couch grass population representing the guerilla type of growth, the translocation of assimilates concerns only the closest (sister) ramets. The phalanx type of growth in couch grass subjected to contamination favours also the accumulation of organic matter and macronutrients (N, Ca) in zones of occurrence of *Agropyron repens* clusters, which are in deficit in areas close to the smelter. The irregular accumulation of heavy metals and the deficit of macronutrients in soil, form near the smelter a patchy environment. In this patchy environment couch grass, as one of few plants, finds appropriate conditions for foraging. The whole of factors in the studied polluted area creates a unique dynamic system between couch grass clones and the local ecological conditions.

KEY WORDS: *Agropyron repens*, heavy metal stress, clonal integration, ^{14}C-assimilate, patchy environment.

INTRODUCTION

Couch grass (*Agropyron repens* (L.) P. Beauv.) as a typical clonal plant shows, according to many authors, a considerable plasticity towards environmental conditions (Håkansson 1982; Cheplick 1998). This feature, among others, hinders the fight with this species as an arduous weed (Cousens and Mortimer 1995). The clonal growth of a couch grass population together with its rich, modular architecture of aerial shoots and rhizomes, the possibility of seasonal dormancy of apical and lateral buds, as well as, the phenomenon of apical dominance make couch grass clones a particularly complex morphological and physiological system of growth and development (Lovell and Lovell 1985; Aldrich 1997). According to recent literature (e.g. Harper 1977; Snaydon 1980; Radosevich and Holt 1984; Bazzaz 1996; Jackson 1997), the physiological, populational and phytocoenotic connections in couch grass – both at individual and populational levels – are still far from full recognition.

Among new studies on physiological reactions of couch grass populations to humidity, level of nitrogen and phosphorus in soil and their influence on the plants' clonal growth, the studies of McIntyre (1987) and McIntyre, Cessna (1998) are worthy of notice. At the same time, most authors recognise the supply of couch grass with nitrogen as the key factor for intensive growth (Ellenberg 1988; Grime et al. 1988). However, these experimental works did not find so far their full development in field population studies, recently intensively conducted on many clonal plants (among others: van Groenendael and de Kroon 1990; de Kroon and van Groenendael 1997; Cheplick 1998; Marshall and Price 1999; Dietz and Steinlein 2001). At the same time, so far field populations of many plants have not been investigated, neither in respect of food foraging during settlement of new territories (compare: Hutchings and de Kroon 1994), nor at the background of the patchy habitat and resource acquisition (Hutchings and Wijesinghe 1997). It seems, that in both the above mentioned problems couch grass makes a perfect though difficult material for study.

During the previous work in the surroundings of the copper smelter Legnica, in the zone of high contamination a distinctly different growth of the couch grass population was recorded (Brej 2000). The data on intensity of pollution and tolerance of couch grass in comparison with the control area are cited after Brej (1998). In the last mentioned area (population K, according to Brej 2000) the tillering of clones led to the origin of a surface pattern of growth of the guerilla type, while the polluted population (A – according to Brej 2000) showed a growth characteristic for the phalanx type strategy. It was assumed that the different pattern of tillering has a strict relation to soil contamination, presence of large amounts of heavy metals (mainly copper, lead, cadmium and zinc), that means, that the phalanx system creates for couch grass clones the possibility to avoid the excess of heavy metals through development of clones in places where the patchy environment is suitable for plants from the point of view: (a) of their vital needs as regards resources, and (b) the patchy toxicity of microhabitats.

The present paper is an attempt to broaden the earlier submitted thesis. A test was undertaken in the contaminated zone near the smelter to document the size and integrity of the clonal structure of couch grass of the phalanx type. Therefore the method of investigation of assimilate translocation with labelled ^{14}C was used. According to the requirements of reliability of population studies and their results the experiment was performed in the field. The paper tries also to answer the question why does the contamination of soil with heavy metals change the clonal growth of couch grass from guerilla to phalanx, and also, whether there are some other factors – particularly trophic ones – influencing the change of phenotypic plasticity of couch grass clones.

MATERIALS AND METHODS

In the year preceding the experiment several m² of surface A (contaminated population) and K (control) were thoroughly weeded to deprive them of below ground parts and above-ground weeds. On these surfaces, at a depth of 10 cm, placed were 10 cm long sections of *Agropyron repens* rhizomes taken from local populations, marking precisely their localisation and direction of growth. Further works were performed from May to July 1997 and were repeated in 1998 in the same area, treating all obtained results as means.

The assimilating individuals within clones of both populations were labelled in the field with ^{14}C to test whether, and how far the accompanying models of clones imported photoassimilates from the „mother" individual and clone. For injections selected were this year's young, but full developed tiller leaves. Used were the previously described field and laboratory experiments with the use of ^{14}C (Colvill and Marshall 1981; Ashmun et al. 1982; Newell 1982; Jónsdóttir and Callaghan 1988; Chapman et al. 1992; Kemball and Marshall 1995), paying particular attention to the few in this respect field studies (see above all, Jónsdóttir and Callaghan 1988). Exposure to $^{14}CO_2$ was performed in the field on one of six clear days. Temperatures ranged from approximately 12-25°C. A single young leaf was enclosed in an air-tight plexiglass chamber of 150 ml volume. $Ba^{14}CO_3$ was mixed with 1 ml of 85% H_2PO_4 to produce $^{14}CO_2$ (Ashmun et al. 1982; Newell 1982). After 1 h, 2 ml of 1 n NaOH was added to absorb any excess $^{14}CO_2$ that had not been taken up by the leaf. The chamber was then removed. All ramets at their parts as well as rhizomes were harvested 14 days after exposure to $^{14}CO_2$ and selected into different morphological parts. The plants were killed immediately in liquid nitrogen, dried, weighted and combusted in a sample oxidiser (B306, Packard Ltd). The $^{14}CO_2$ released by combustion

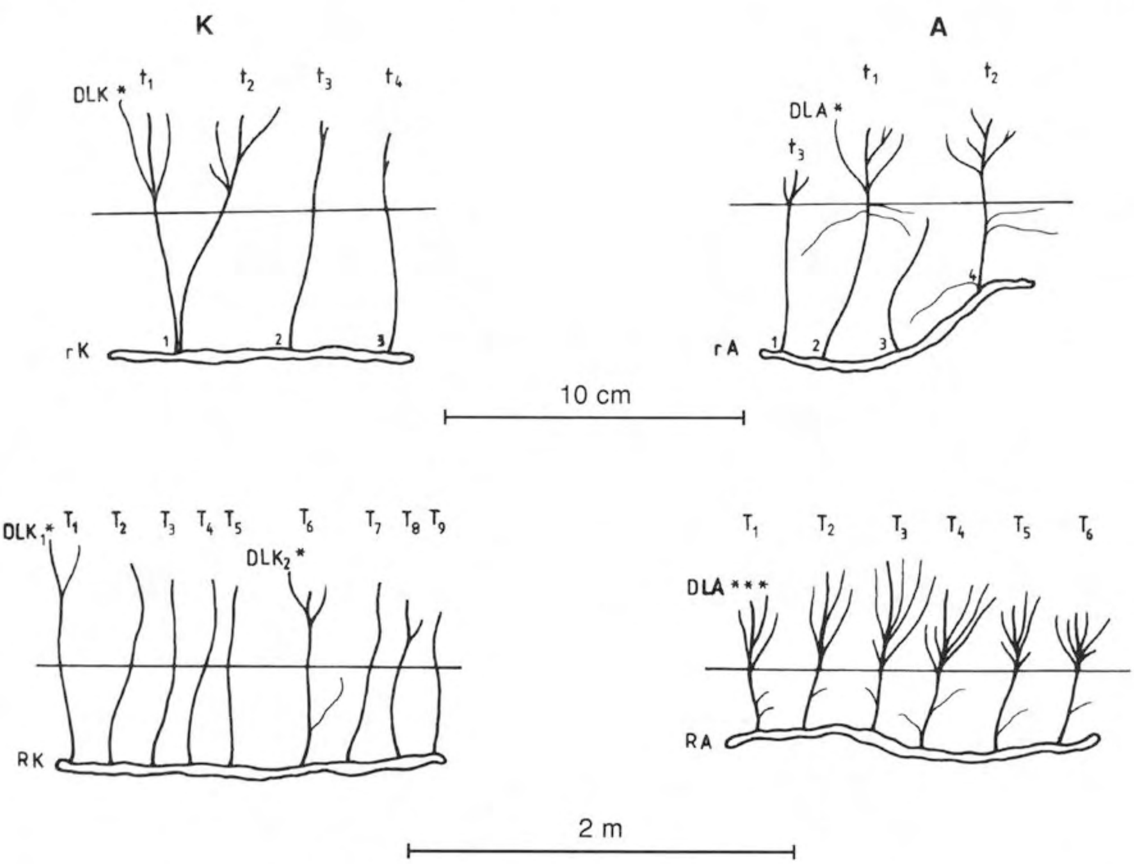


Fig. 1. A diagrammatic position at which individual leaves were supplied with $^{14}CO_2$ in experiment 1 (top) and experiment 2 (below). Experiment 1 shows the movement of assimilates between close connected ramets in two populations (A and K), while experiment 2 illustrates the movement of assimilates in a larger scale between ramets in unpolluted (K) and polluted (A) populations. An asterisk and letters DLK and DLA mark the labelled leaves. Letters t, r and T, R indicate tillers and rhizomes analyzed respectively in experiment 1 and 2, while numbers 1-9 indicate samples analyzed after labelling.

was absorbed in a strong base and counted in a liquid scintillation counter (Beckman LS-150C). The counting efficiency was 85%. Each treatment had at least four replicate plants. The total N concentrations in the soil were analysed in a Carlo-Erba NA1500 Analyzer, while KCL extractable NH_4-N and NO_3-N in a Braun-Luebe system analyser (Schulze 2000). The content of extractable soil calcium was determined by the use of AAS method (Allen 1989).

RESULTS

Experiment 1

The purpose of this experiment was to follow the movement of assimilates within the closest tillers in clone, probably the so-called „sister" tillers, growing from the nearest rhizome nodes. Owing to the precise excavation of the below ground parts and their analysis it was possible to select not only the nearest tillers, but also fragments of rhizomes important for coming to the conviction on acropetal movement of the assimilates. An important result is the persistency of the highest accumulation of assimilates in population K and A in leaves of the labelled tillers (DLK and DLA), particularly visible in population K (DLK), of which the remaining tillers obtained only from 5 to 20% of the labelled assimilate (Figs 1, 2). This evidences the rapid gain of independence of most of the tillers within the clone on uncontaminated soil. The axillary buds had there an equal start and gave rise at the same time to many shoots within the clone. The contaminated population A showed a completely different strategy of assimilate distribution. Apart of the mother tiller, accumulating 30% of assimilates, the remaining tillers got an equal amount of assimilates (on average 10%), whereas by a half more obtain shoots situated at the border of the cluster t_3 (Fig. 1). The assimilates in population A expand successfully in rhizomes which obtained as much as 50% of labelled assimilates (rhizomes of population K obtained merely 14% of the assimilate). Worthy of notice is also the content of the most distant section of rhizome from place of its labelling, which in the contaminated population (A) stored up as much as 19% of the assimilate.

Experiment 2

This experiment shows the distribution of the assimilate in couch grass ramets ca. 2 m long. Its aim was to depict the movement of assimilates in clonal structure typical for the studied populations K and A. The regular and equally dense surface structure of population K is typical for fallow grounds with couch grass from uncontaminated areas. A denser one (A), with connected tillers situated close one to another, almost loose clusters, developed only closest the smelter, in places highly contaminated with heavy metals. The habit of population A has been qualified as a specific defence strategy in stress conditions. It resembles the clonal strategy of the guerilla type (Brej 2000). Figure 3 gives us an outlook upon the specificity of assimilate distribution existing in population A, contaminated with heavy metals. After labelling as much as 40% of the assimilate are transferred to tillers (T_4, T_5), distant by almost 1.5 m, and, though minimal (5%) amount, to consecutive tillers, situated ca. 1.9 m from the place of ^{14}C application. Of course, this basipetal transport must be connected with the earlier acropetal movement from tillers to rhizomes. Because of methodological reasons (difficulties with separation of the „proper" rhizome) the presence of assimilates has been ascertained only in rhizome 35 cm away from the tiller (DLA) administered with ^{14}C. The results of nitrogen and calcium contents shown in Fig. 4, presenting the state of soil nutrients in the vicinity of the smelter, will be discussed in the next chapter.

DISCUSSION

The presented results, obtained in field by means of the method of labelled assimilates, evidence the long lasting in

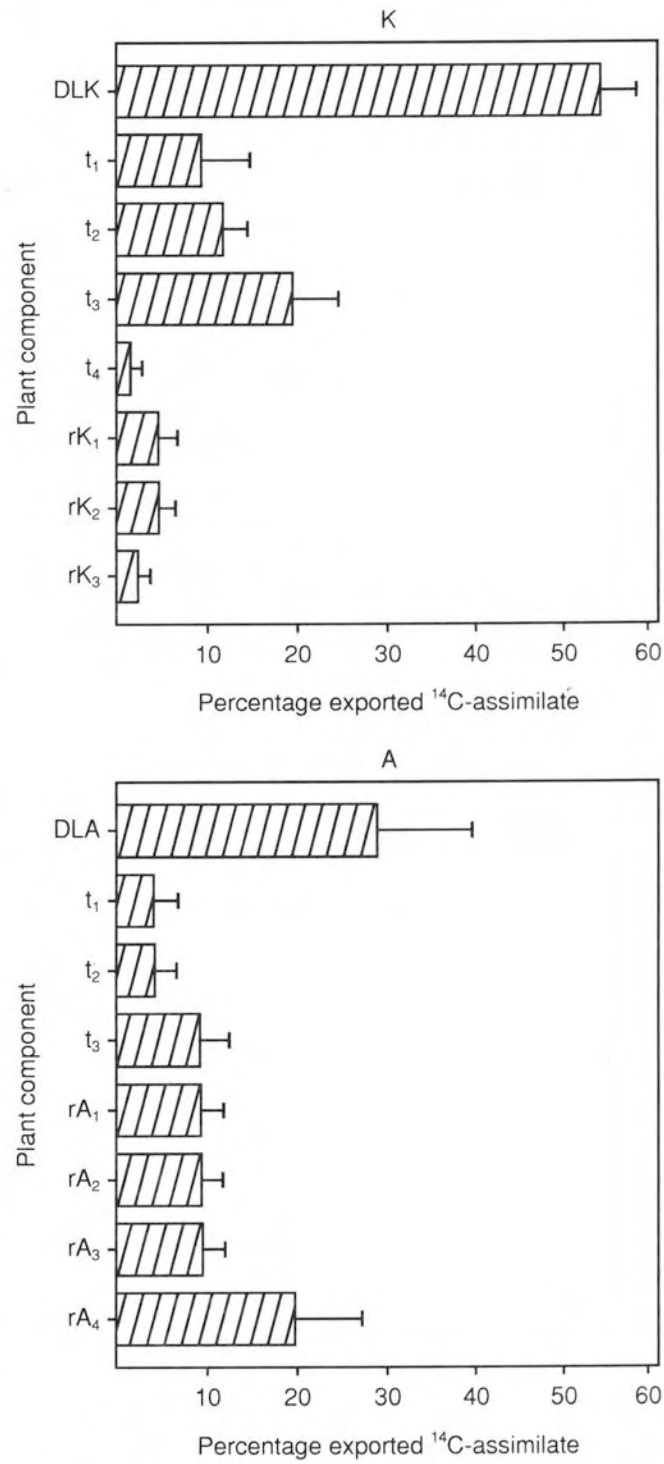
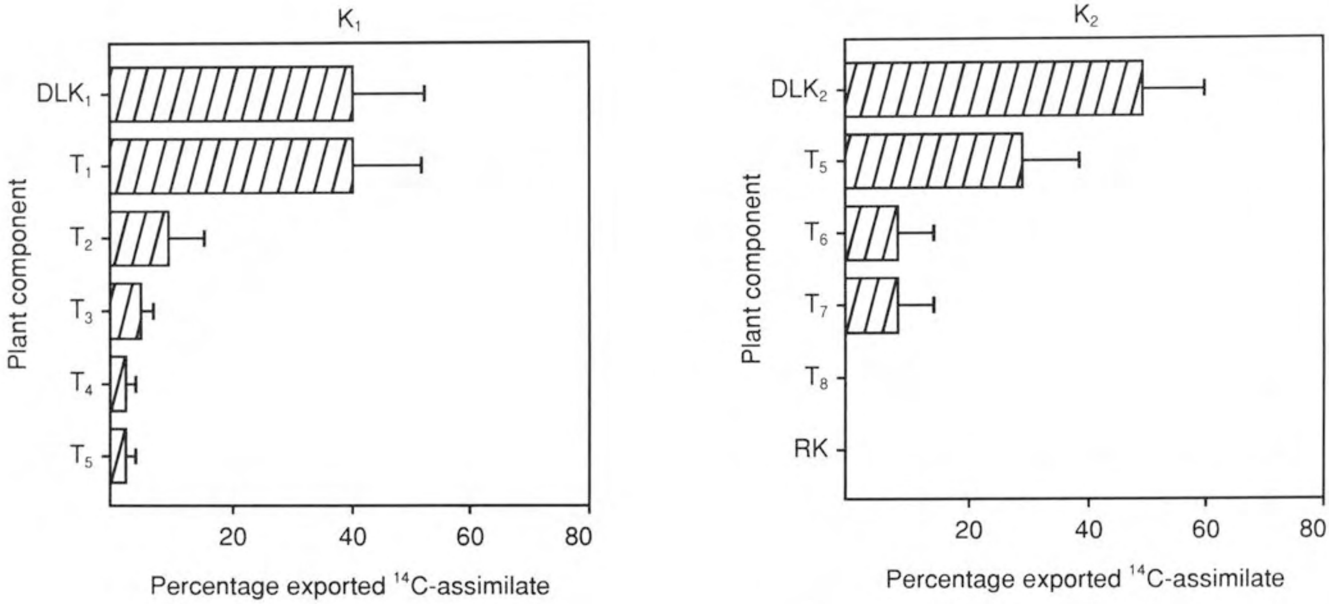


Fig. 2. Experiment 1. The distribution of exported ^{14}C-assimilates from individual leaves to close connected ramets (± SE) in unpolluted (K) and polluted (A) populations. For explanation of tillers and rhizomes see Fig. 1.



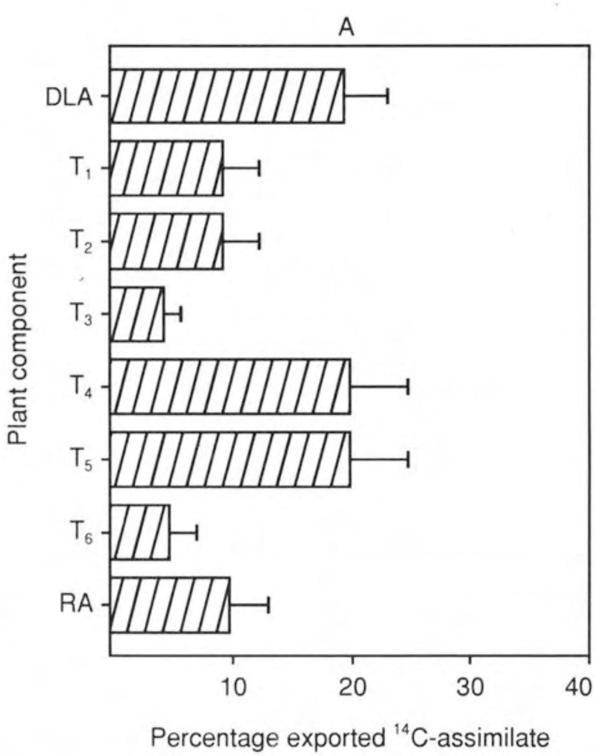


Fig. 3. Experiment 2. The distribution of exported ^{14}C-assimilates from individual leaves to more distant ramets (± SE) in unpolluted (K) and polluted (A) populations. K_1 and K_2 indicate the results for two places of labelling (DLK_1 and DLK_2).

couch grass connections between tillers within a clone, particularly in stress conditions (population A). The interclonal connections in plants and the exchange of the assimilate are known for a long time. They are characteristic particularly for rhizomatous grasses and sedges (Allessio and Tieszen 1978; Colvill and Marshall 1981; Jackson et al. 1985; Jónsdóttir and Callaghan 1988), and for perennial herbs (Ashmun et al. 1982; Newell 1982; Hartnett and Bazzaz 1983; Pitelka and Ashmun 1985; van Groenendael and de Kroon 1990; Chapman et al. 1992; Kemball and Marshall 1995; de Kroon and van Groenendael 1997). The translocation of the assimilate in couch grass was investigated only in laboratory conditions (Forde 1966; Rogan and Smith 1974), mostly to investigate the range of effects of various herbicides (Coupland 1985; Bruce et al. 1993). There is no settled view on conditions in which the interclonal connection is maintained, and what are its advantages for plants. At present more and more frequent are papers giving information on the specific division of labour in clonal plants (Hutchings and Wijesinghe 1997), particulary concerning the foraging of mineral supply (Sutherland and Stillman 1988; Cain 1994) and proper humidity and light conditions (Slade and Hutchings 1987). Among papers concerning that problematics of special interest are those devoted to stoloniferous plants *Glechoma hederacea* (Birch and Hutchings 1994) and *Trifolium repens* (Chapman et al. 1992). From among other theoretical papers worthy of notice are model investigations (Cain et al. 1996), considerations devoted to the plasticity of clonal plants (Taylor and Aarssen 1988; de Kroon et al. 1994) and clonal integration and segmentation (Birch and Hutchings 1994). Confronting the results of many authors with own investigations one should stress that, despite the considerable plasticity of clonal plants, their interclonal connections are not stable and depend on suitable ecological conditions. In case of the described here couch grass populations, for production and durability of interclonal connections responsible is, above all, the environmental stress caused by the excess of heavy metals in soil. The role of the stress factor in formation of permanent interclonal connections had already been formerly noticed, ascribing a high significance e.g. to defoliation caused by grazing and other disturbances (Ashmun et al. 1982; Newell 1982).

In the investigated couch grass population (A) as stressing conditions also the shortage of macronutrients can be taken into account. Many authors emphasise the crucial part of suitable soil humidity and high contents of nitrogen and calcium for developmental success of couch grass (McIntyre 1972; Leakey et al. 1975; Rogan and Smith 1975; McIntyre and Cessna 1988). The area in the vicinity of the copper smelter is not fertilised and makes a fallow ground. Besides, it is known that couch grass is recognised as an extravagant consumer of nutrients (Werner and Rioux 1977). Known is particularly the high demand of this plant for nitrogen, confirmed both in laboratory and field experiments (Mortimer 1984; McIntyre and Cessna 1998; Pałys 1990). Figure 4 shows the local nutrient situation in the vicinity of the copper smelter. Here the habitat occupied by

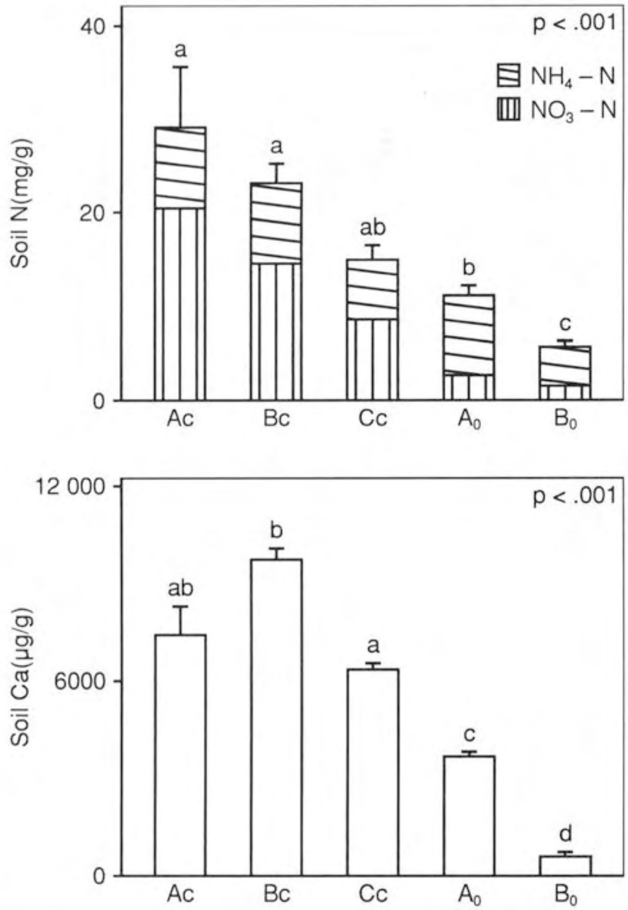


Fig. 4. Contents of soil N and Ca in three densed *Agropyron repens* populations (Ac, Bc, Cc). For comparison contents of N and Ca in soil devoid of plants (Ao, Bo) are given. Mean of four replications in 1998. Location of populations A, B, C – see Brej 1998.

couch grass has a soil of average fertility in nitrogen and calcium – both the elements very important for *A. repens* life. A specific analysis of local distribution of nutrients near the smelter enabled to find that it is typically patchy, with more nitrogen – both nitrate and ammonium – and calcium accumulated in zones of occurrence of *Agropyron repens* clusters than beyond them. Acid rains are also an important source of anthropogenic nitrogen in the area of the smelter (Fabiszewski et al. 1986). According to data of the copper smelters' Department of Environment Preservation, they provide ca. 40 kg N/ha/year – data for 1998. Within the cluster surface there is usually twice as much nitrogen and much more calcium (two to three times more) than beyond the plant clusters (Fig. 4). This patchy distribution of nutrients is known in ecological literature as „island of fertility" (Schlesinger et al 1996; Berendse et al. 1999) in a nutrient-deprived matrix as one of the important type of environmental heterogeneity (Caldwell and Pearcy 1994; Huber-Sannwald and Jackson 2001). Plants forming similar clusters retain much more nutrients than in areas usually devoid of vegetation. Moreover, these plants accumulate humus through decomposition of litter, enriching the soil by nutritive compounds, improve its structure and enable a more effective water supply. Such properties are extremely important in conditions the copper smelter, as the physical structure of soil devoid of vegetation does not favour the accumulation of water, and in result of excess of heavy metals is also devoid of biologically active humus. Moreover, humus binding heavy metals in chelate compounds, inactivates in a peculiar manner the mentioned above islands of fertility from the toxic excess of metals (Brej 1998). Thus, in the patchy environment as a result of the smelter's influence on soil environment (heavy metals), couch grass contributes to the „improvement" of its own patches, which include a more fertile and less toxic soil. In this way a stable system between couch grass and the toxic environment is formed. This environment could have been settled in the first stage by couch grass, owing to the arisen tolerance mechanisms to heavy metals in some populations of this plant (Brej 1998). Later, between clones of *A. repens* and the soil, mechanisms of stable balance are formed. Owing to the tolerable trophic conditions, this balance enables some of the clones to survive for several years in the area under discussion. The clonal growth enables the populations to react flexible to the pollution emitted by the smelter. This consists in creating growth forms of the phallanx type. These forms, as shown above, enable the interclonal supply with assimilates, facilitating the life of populations in bigger clusters. This phenomenon fastens also the patchy structure of the clone. In the zone closest to the smelter the share of other plants is minimal. The success of couch grass in stress conditions near the smelter has, recapitulating the own studies, the following mutually connected conditionings:

1) Ecophysiologic ones, consisting in the rapid, ca. 30 years lasting process of formation of populations resistant to the most toxic heavy metals (copper, lead, cadmium, zinc)

2) Morphologic-plastic ones, consisting in the possibility of forming populations of the phallanx type growth structure

3) Integrational-clonal ones, consisting in a rather long maintenance of interclonal connections in rhizomes, what ensures a long lasting flow of assimilates between ramets and whole neighbouring clones. This is the way the clones „help" each other in stress conditions and can thus reach an age of seven years. From an agronomic point of view, the „starving" fallow land populations can create the rise of clonal forms particularly difficult for mechanical fighting. On the other hand, the long lasting wandering of nutrients (acropetal and basipetal) existing in this plant creates a way to fight this weed chemically (Bruce et al. 1996). This can consist in using smaller amounts of herbicides, which block the physiological processes of couch grass or inhibit its meristematic tissues.

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EKOLOGICZNE SKUTKI TRANSLOKACJI ASYMILATÓW W KLONACH PERZU *AGROPYRON REPENS* WYSTĘPUJĄCYCH W SĄSIEDZTWIE HUTY MIEDZI LEGNICA

STRESZCZENIE

W warunkach oddziaływania huty miedzi Legnica badano w terenie powiązania nadziemnych części wegetatywnych perzu (tylerów) i rozłogów metodą translokacji asymilatów z zastosowaniem ^{14}C. Stwierdzono, że stresowe działanie nadmiaru metali ciężkich wpływa na plastyczność fenotypową perzu, poprzez formowanie bardziej skupiskowego wzrostu klonalnego typu falangowego (phalanx). Wzrost bardziej skupionych klonów podtrzymuje stwierdzona u nich znaczna integracja fizjologiczna, pozwalająca na transport asmilatów na odległość do 1,9 m. Przekazywanie asymilatów odbywa się zarówno w kierunku rozłogów, jak i z rozłogów do bardziej odległych pędów nadziemnych. W nieskażonej (kontrolnej) populacji perzu, która reprezentuje strategię wzrostu i rozwoju typu guerilla, stwierdzono przekazywanie asymilatów tylko do najbliższych części klonu. Znamienny dla bliskiego otoczenia huty wzrost falangowy perzu sprzyja gromadzeniu się w obrębie kęp substancji organicznej i większej ilości makroskładników (N, Ca) – deficytowych w sąsiedztwie huty. Nierównomierna kumulacja metali ciężkich w glebie i niedobór makroelementów tworzą w rejonie oddziaływania huty środowisko mozaikowe, w którym wyspecjalizowane populacje perzu znajdują odpowiednie warunki do osiedlania się i odżywiania (tzw. foraging). Sukces perzu w miejscowych warunkach stresowych wynika z uwarunkowań ekofizjologicznych (wytworzenie populacji tolerancyjnych na niektóre metale ciężkie), morfologiczno-plastycznych (struktura wzrostu typu phalanx) i integracyjno-klonalnych (utrzymywanie połączeń interklonalnych w celu przekazywania asymilatów dalej położonym pędom i całym klonom). Z rolniczego punktu widzenia ugorowe, „głodowe" populacje perzu mogą kreować powstanie form klonalnych szczególnie trudnych do zwalczania mechanicznego. Z drugiej strony, istnienie u tej rośliny w systemie pędów nadziemnych i podziemnych długo utrzymującej się wędrówki składników pokarmowych (acropetalnej i basipetalnej) stwarza drogę do walki chemicznej z chwastem. Może ona polegać na zastosowaniu małych ilości substancji toksycznych, które – rozprowadzone drogą wewnętrzną – będą skutecznie blokować procesy fizjologiczne perzu i niszczyć jego tkanki merystematyczne.

SŁOWA KLUCZOWE: *Agropyron repens*, wpływ metali ciężkich, integracja klonalna, ^{14}C, asymilaty, środowisko mozaikowe.