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Morphological plasticity in the rhizome system of Solidago gigantea Ait. (Asteraceae): comparison of populations in a wet and a dry habitat

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Abstract

This study was motivated by the fact that although the plasticity of its above-ground organs is obvious in natural conditions and there are many data on the plasticity of *Solidago*'s rhizome system in glasshouse experiments, there are no data on below-ground plasticity under natural conditions. We compared the morphology of rhizomes in two, contrasting habitats. We found that rhizome system responded to environmental conditions: in the dry habitat, ramets developed more but shorter rhizomes compared to the wet habitat. The decrease in rhizome length can be explained by the decrease in the size of above-ground organs, but the increase of rhizome number cannot. The most important regulating factor of rhizome growth is probably its mechanical restriction by the root biomass of other species.

Introduction

Morphological plasticity is the ability of a species to change the shape and size of its organs when grown under different environmental conditions. This phenomenon is well known in plants, for example the morphological differences between sun-grown and shade-grown individuals of a particular species. This feature is so peculiar in some free-floating aquatic plants that different 'growth forms' of a particular species are often scarcely recognisable as belonging to the same species (Ashton & Mitchel 1989). The high morphological variability allows a species to compete for a wide range of habitats (Shorina & Smirnova 1985; e.g. Ashton & Mitchel 1989).

There are many clonal plants among the most successful plant species including dominant species of several habitats and successional stages (Sebsen & Thorne 1985; Callaghan et al. 1992; Prach & Pyšek 1994), widespread weeds (Leakey 1981) or invasive species

(Thompson 1991; Pyšek 1997; Balogh et al. 2003). Some clonal species follow strict constructional rules (e.g. Bell 1979; Noble et al. 1979), while others can alter their clonal growth (see review in Kroon & Hutchings 1995) in response to their abiotic environment (e.g. Slade & Hutchings 1987a; Slade & Hutchings 1987b), intensity of competition (e.g. Hartnett & Bazzaz 1985a) or type of competitor (e.g. Schmid & Bazzaz 1992).

At fine scale, the plastic placement of ramets can increase the proportion of ramets in favourable microsites (Sutherland & Stillman 1988), but the optimal strategy depends on the spatial and temporal predictability of the environment (Oborny 1994). At coarse scale, plasticity yields differences in species demography across communities.

Solidago gigantea is a successful invasive species in large regions of Europe (Weber 1998). In Western-Hungary it occurs in different habitats from the edges of swamps to dry grasslands (Botta-Dukát 1994; Botta-Dukát & Dancza 2008). Plasticity of the aboveground organs is obvious. In wet habitats, *S. gigantea* forms monodominant patches, where shoot height, shoot density and the proportion of flowering shoots are high. In dry habitats, it co-occurs with other species (primarily different grasses); shoot height, shoot density and the proportion of flowering ramets are low. There is little information on the plasticity of rhizome system. Although previous studies, based on glasshouse experiments, reported that the rhizome system of *Solidago* species responded to environmental conditions (Hartnett & Bazzaz 1985a; Hartnett & Bazzaz 1985b; Schmid & Bazzaz 1990; Schmid & Bazzaz 1992), we have only little information about its importance in natural conditions (Alpert 1995).

Therefore, our study aims at answering the following question: „Is there any plasticity in the geometry of *Solidago gigantea* rhizome system in natural conditions?" Two sites were chosen to represent two typical communities where *Solidago* occurs: edges of swamps and dry grasslands.

Coleman et al. (1994) pointed out, that size of the whole plants has to be considered when studying plasticity in size of organs. Thus, we asked whether plasticity in rhizome number and rhizome length could be interpreted as a consequence of different ramet size in the two sites.

Materials and Methods

The study species

Solidago gigantea Ait is a rhizomatous perennial of North American origin (Weber 1998; Botta-Dukát & Dancza 2008). It appeared in the Carpathian Basin about 150 years ago (Moesz 1909). Since then it spreads quickly (Dancza & Botta-Dukát 2000), and it is considered nowadays as one of the most important invasive plant species in Hungary (Török et al. 2003). According to definitions of Richardson et al. (2000) *Solidago gigantea* is a transformer, because in favourable habitats it forms a large, dense, monodominant patches and destroy the original vegetation.

Its rhizome growth is sympodial; shoots develop from the axillary bud of the rhizomes (Fig. 1), and new rhizomes are initiated at the base of the stems (Almádi et al. 1997). The aboveground portion of ramets dies in October-November, and their daughter rhizomes remain dormant until the following spring. Contrary to the congeneric *Solidago altissima*, whose rhizome connections persist for up to five years (Cain 1990), we did not find rhizomes older than two years. Only sister ramets were connected through their common mother ramet, and no other interconnections occurred. At the time of study, there were two generation of rhizomes: rhizomes which developed in the previous year and now connect the sister ramets (below they will be called old rhizomes), and rhizomes which developed in that year (below they will be called new rhizomes).

Study sites

Two significantly different habitats were chosen to this study: a dry site with low density of *Solidago* and a wet site with high density of *Solidago*.

Both sites were near Keszthely, in the Kis-Balaton region (Balatonfelvidék National Park). The region is mostly covered by wetland vegetation (e.g. reed and sedge communities). At higher elevations, there are sand dunes with steppe vegetation (Szabó et al. 1998). The dry site was such a sand steppe at about 108 m a.s.l. Its dominant species were *Festuca rupicola*, *Carex hirta* and *Botriochloa ischaemum*. The wet site was situated about 50 m from here at about 105 m a.s.l. Due to lower elevation the availability of water was significantly higher here. The vegetation represented an ecotone between sand steppe and the swamp. In this zone, *Solidago gigantea* formed monodominant stands where no other species occurred.

In the dry site, we assume that the major limiting factors are lack of water and nutrients. Roots of co-occurring species create a dense mat in the soil at the depth where *Solidago* rhizomes run. This suggests that they compete for water and nutrients. Limitation by the shortage of light was probably negligible since the *Solidago* density was low (Table 1) and the co-occurring species were shorter than *Solidago* (height of co-occurring species was 20-40 cm, height of *Solidago* was 80-100 cm).

In the wet site, water and soil nutrients were ample and the density of *Solidago* shoots was rather high. Therefore we assume that here the most important limiting factor was light.

Sampling and data analysis

To characterize the sites we used shoot density, shoot height and proportion of flowering shoots. Shoot density was counted in 20 0.5x0.5m plots before destructive sampling. The shoot height was measured and number of flowering shoots was counted in the shoots excavated for the study of rhizome system. The differences in shoot density and shoot height were tested by Mann-Whitney test (Zar 1999). The proportions of flowering shoots in two sites were compared by G^2-test (Sokal & Rohlf 1981).

In end of August 1999, in both sites all shoots were excavated from about a 2 m^2 area. The architecture of rhizome system of Solidago gigantea is intermediate between „compact” and „spreading” type (Schmid & Bazzaz 1987). It means that this species does not form monoclonal patches but different genets intermingle. On the basis of this fact, the excavated shoots probably belong to several genets. In that time the rhizome growth probably had not finished yet (Werner et al. 1980). However, after fruiting when the rhizome growth have finished, shoots easily separete from the below-ground part of ramet, therefore the whole ramet cannot excavated. This earlier sampling date probably does not cause a problem, because there were no phenological differences between sites and in a previous study we had got same differences between sites based on rhizomes developed in the previous year and rhizomes developed in the year of study harvested in July (Dancza I. and Botta-Dukát Z. unpublished data).

At the border of the excavation area, the rhizome system of the shoots became damaged considerably. Therefore, these shoots were excluded from the subsequent analysis. 150 and 137 ramets were involved in the analysis in the wet and dry site respectively. The complete rhizome systems (the connected sister ramets and their new rhizomes) could not be excavated in the dry site. Therefore we measured only the new rhizomes.

To investigate the degree of plasticity, geometry of rhizome systems was compared between sites. The geometry of rhizome systems was characterized by the number of new rhizomes and relative position of their apical bud. It is important that daughter ramets will develop from the apical buds of the new rhizomes. It means that number of new rhizomes determines the possible number of daughter rhizomes and position of apical buds determines the position of daughter ramets.

Number of new rhizomes was counted in each excavated ramets. Ramets were categorized according to the number of rhizomes developed from their basal part. The shoots with four or more rhizomes were merged into one category to satisfy the assumptions of the test-

In each new rhizome, two variables were measured: length and branching angle (angle between new and old rhizomes; Fig. 2.). These two parameters describe unambiguously the position of a daughter ramet relative to its mother.

The apical bud of some rhizomes broke down during excavation. From the statistical point of view, it means that rhizome length is a right-censored data. Therefore, we applied two non-parametric tests that are often used in survival analysis: log-rank test and Gehan-Wilcoxon test (Pyke & Thompson 1986). The distributions of branching angle were compared by Watson’s U^2-test (Zar 1999).

In another analysis, the shoots were divided into two height classes by splitting at average in each site. The two classes were compared within the two sites separately. By this way, relatively tall and supressed, relatively short shoots were compared in each site disregarding the average shoot size of sites. The same tests were performed between classes as used earlier in the between-site comparison. This let us separate the effect of size from the effect of habitat differences.

Results

Comparisons between sites

Comparison of the two sites showed that the density of *Solidago* was smaller (Mann-Whitney U=5.00; p<0.001), the shoots were shorter (Mann-Whitney U=4431; p<0.001) and the proportion of flowering shoots was lower (G^2=4.7; p=0.03) in the dry site (Table 1).

The distributions of rhizome numbers were significantly different in the two sites (G^2=59.56 p<0.001). In particular, the proportion of ramets with only one daughter rhizome was higher, and the proportion of ramets with three or more daughter rhizomes was lower in the wet site (Fig. 3).

Although there were short rhizomes in both sites (Fig. 4.), the average rhizome length was significantly higher in the wet site (log-rank test: $\chi^2=4.66$, $p<0.001$; Gehan-Wilcoxon test: $W=3.63$, $p<0.001$).

We found a significant difference between the two sites in the distributions of branching angles ($U^2=0.1919$ $p\approx0.045$). But the significance of this small difference can probably be attributed to the relatively large sample size (there were 292 and 208 new rhizomes in the dry and wet site, respectively) rather than to any biological difference (Fig. 5).

Within sites comparisons

Taller shoots developed more rhizomes in both sites ($G^2=14.75$, $p<0.01$ in the dry site; $G^2=15.97$, $p<0.01$ in the wet site; Fig. 6). In the wet site, the rhizomes of tall shoots were longer than the rhizomes of short shoots (log-rank test 5.26, $p<0.001$; Gehan-Wilcoxon test: $W=4.83$, $p<0.001$; Fig. 4.). In the dry site, there was no significant difference (log-rank test 0.82, $p=0.2$; Gehan-Wilcoxon test: $W=0.002$, $p=0.49$; Fig. 4.).

Discussion

Variation in natural communities

Both rhizome numbers and rhizome lengths were significantly different in the two habitats (Table 2). This confirms the results of earlier glasshouse experiments: there is plasticity in the geometry of *Solidago*'s rhizome system in natural conditions.

Cain (1991; 1994) pointed out that the long-term consequence of different rhizome lengths in terms of net displacement of the clone strongly depends on the distribution of branching angles. In our case, however, the distribution of branching angles proved to be constant.

Possible explanations for the differences

In the dry site, where the average shoot height was lower, shoots developed more rhizomes than in the wet site. On the other hand, within both sites, taller shoots developed more rhizomes (Table 2). This contradiction suggests that the difference between sites in rhizome number was „real" plasticity, not only a consequence of different sizes of aboveground shoots.

The two sites differed in the rhizome lengths of short vs. tall shoots. In the wet site, the rhizomes of taller shoots were longer. If the same trend existed in the dry site too, this could have explained the differences between sites. In the dry site, however, rhizome length was not influenced by shoot height. Some other factor prevented tall shoots from developing long rhizomes. This factor may be, for example, the dense root system of coexisting species, which can mechanically restrict rhizome growth (c.f. Schmid & Bazzaz 1990; Schmid & Bazzaz 1992). Apical buds of developing rhizomes may hinder the initiations of new rhizomes. When the rhizome growth stops, for example because it is mechanically restricted, apical dominance decreases and new rhizomes can be initiated. This is a possible explanation to the higher number of rhizomes in the dry site.

Consequences of the differences

After establishment, *Solidago* propagates almost exclusively by rhizomes (Cornelius 1990). Thus, the number and length of rhizomes are very important life-history parameters, and the observed differences may have important consequences on the competitive ability:

(1) More intensive integration within genets in the dry site

Comparing *Solidago canadensis, S. gigantea* and *Aster* spp., Schmid and Bazzaz (1987) (1987) found a negative correlation between average rhizome length and the level of within-genet integration. This rule may hold within a species, too, because transport is easier to shorter distances.

According to the diversity of co-occurring species, the dry site was more heterogeneous. Integration among shoots decreases the effect of this heterogeneity on genet performance (Hartnett & Bazzaz 1985a). Thus, integration can be very advantageous in the dry site, whenever averaging of microhabitat conditions over more than one ramet is favourable.

(2) Quick sprouting in the wet site

In spring, new ramets obtain resources from the rhizomes. Large rhizomes may be able to support more rapid ramet growth. Quick sprouting may be relatively more advantageous in the wet site, where light is a major limiting factor. Earlier studies (Goldberg 1988; Cain 1990; Stoll et al. 1998)have shown that in the case of other *Solidago* species (*S. altissima* and *S. canadensis*), there is positive correlation between parent rhizome length, ramet size, chance of survival and chance of flowering. Thus, it can be hypothesized that the production of long rhizomes is adaptively advantageous.

(3) Populations avoid overcrowding in the wet sites

Meyer and Schmid (1999) suggested that "genets of *Solidago altissima* would prevent intraclonal crowding by producing longer but fewer rhizomes as they increased in size". If the ramets are not strongly integrated, then the number of rhizomes is decided at ramet rather than genet level. This mechanism would prevent not only intraclonal but also even intraspecific crowding. Earlier experiments (Hartnett & Bazzaz 1985b; Schmid et al. 1988) did not find any clear relationship between ramet density and rhizome structure. In our study, the density correlated positively with rhizome length and negatively with rhizome number. The comparison between short and tall ramets at the same site suggests that this is probably a consequence of mechanical restriction and not a mechanism to avoid overcrowding.

Which environmental clues may control the response of rhizomes to below-ground competition?

Schmid and Bazzaz (1992) suggested that 'guerrilla' and 'phalanx' species responded differently to competition. 'Guerrilla' species tend to respond by decreased rhizome number and increased rhizome length, whereas 'phalanx' species respond to competition by increased rhizome number and decreased rhizome length. Although, the term 'guerrilla' and 'phalanx' are always relative, *Solidago* species rather belong to the second group. They supposed that the most important effect of the competitors is the depletion of resources and this clue controls the response of rhizomes (Schmid & Bazzaz 1992). In experiments, fertilisation did not have any significant effect on the rhizome structure of *Solidago* (Schmid & Bazzaz 1992). In the same experiment, the type of competitor species had a significant effect (e.g. in the dense root mat of *Poa*, *Solidago* developed more but shorter rhizomes). It is possible that the morphological response in some rhizomatous 'phalanx' species cannot be attributed to environmental clues (as supposed by Schmid & Bazzaz 1992) but mechanical restriction of rhizome growth.

Plasticity and invasiveness

Ecologists interested in biological invasions have repeatedly attempted to answer the question: what sort of traits are specific to invasive species (e.g. Kolar & Lodge 2001; Fenesi & Botta-Dukát 2010)? Most authors concentrated on the „average" of life history traits and variation of traits within species has usually been neglected (except in Ashton & Mitchel 1989). Plasticity can be of great importance, because the same property may be advantageous in one habitat but disadvantageous in an other. *Solidago gigantea* occurs in very different habitats, and its morphological plasticity may facilitate its wide distribution and high invasiveness.

Conclusions

Although only two sharply different habitats were compared in this study, these sites were chosen to represent two typical habitats of *Solidago.* Thus, in spite of autocorrelation of data, the results allow to say that there is plasticity of below-ground organs in natural conditions and to generate well-established hypotheses on its causes and consequences. Of course, these hypotheses have to be tested by experiments and further field studies are needed to evaluate the relationship between habitat and rhizome morphology in detail.

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Table 1. Some important features of *Solidago* populations in the two studied sites

	Dry site	Wet site
Shoot density (shoot/m^2, average±SD)	74.8±4.65	145.6±7.89
Shoot height (cm, average±SD)	102.2±19.84	134±31.96
Proportion of flowering shoots (%)	21.9	33.3

Table 2: Summary of the results. < and > indicate significant differences, while ≈ indicate that there were no significant difference

	Between sites	Within sites	
	dry site wet site	dry site	wet site
Shoot height	<	short tall	short tall
Rhizome number	>	<	<
Rhizome length	<	≈	<

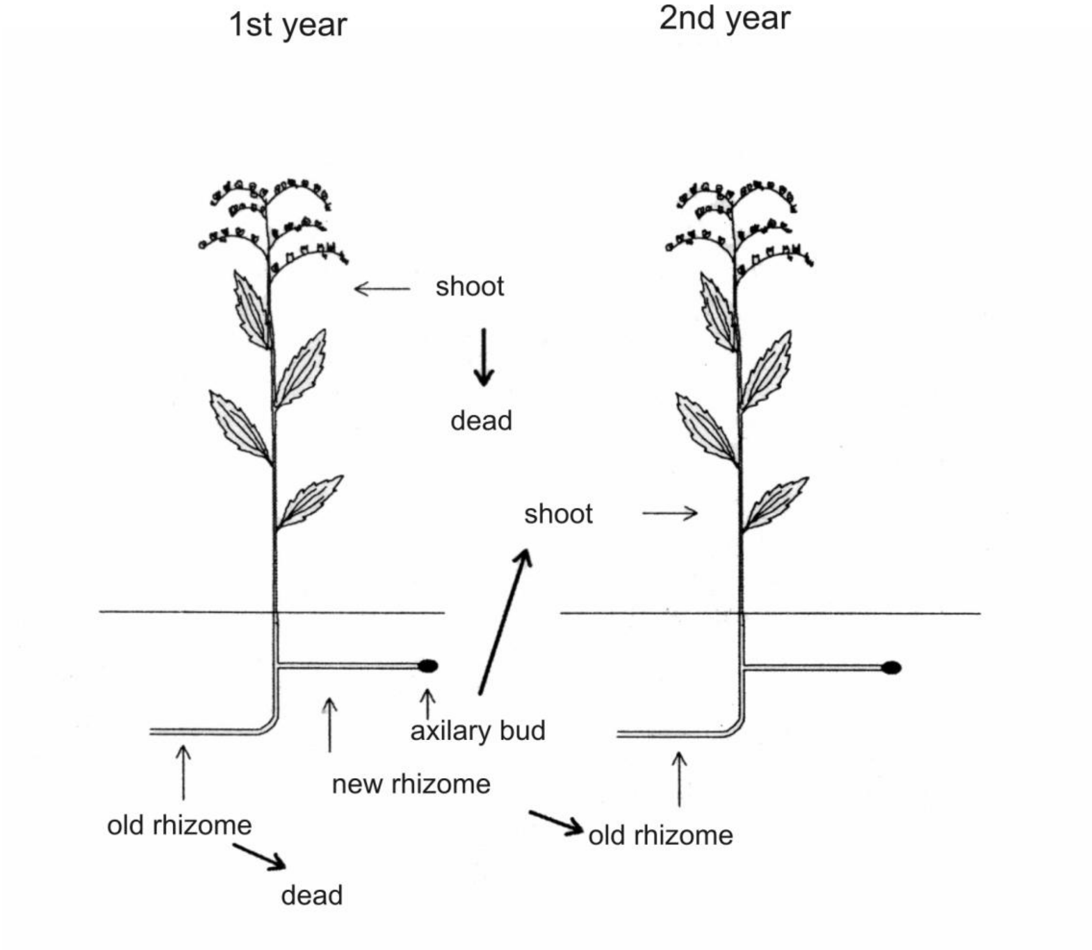


Figure 1: Vegetative reproduction of *Solidago gigantea* (bold arrows indicate ontogeny)

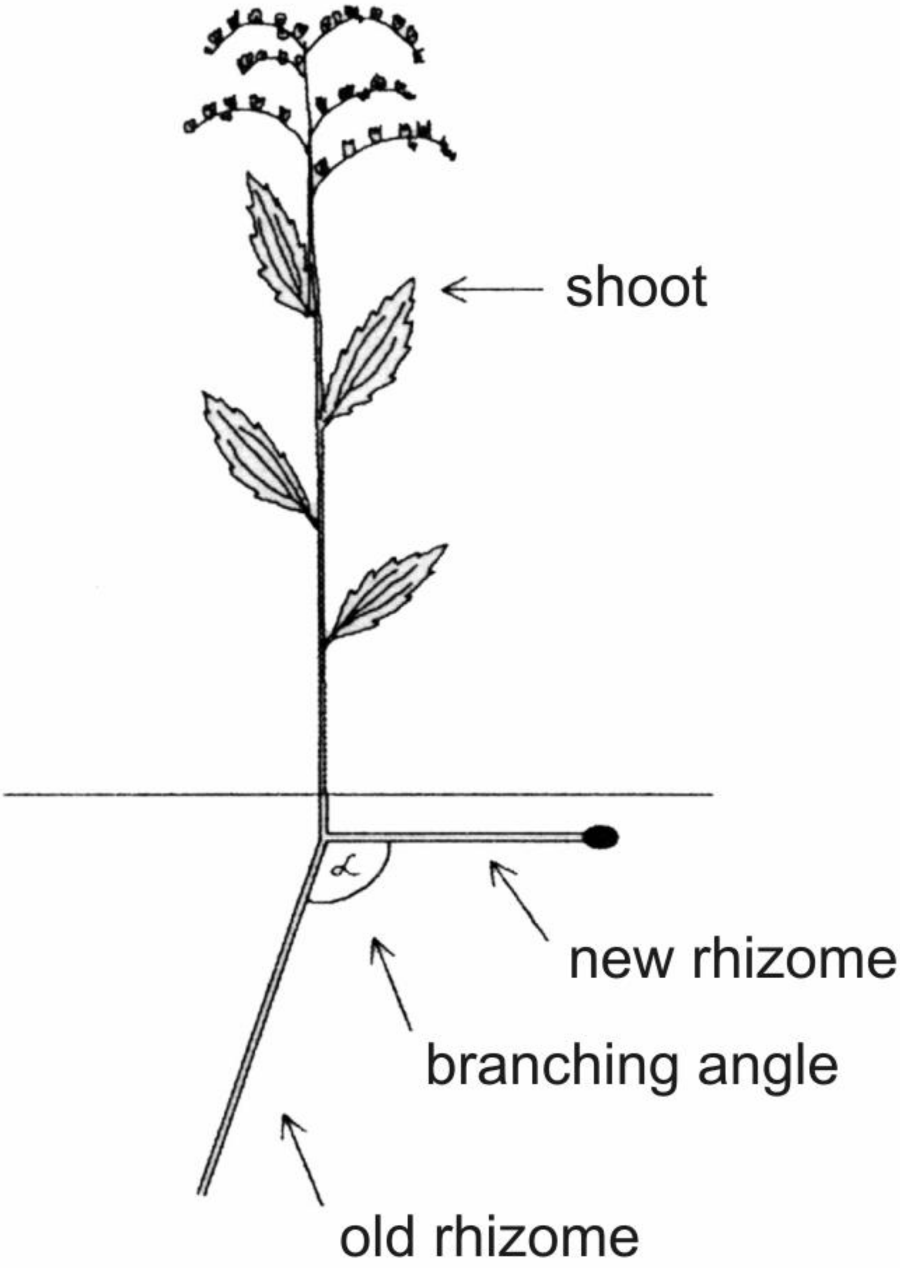


Figure 2: Definition of branching angle

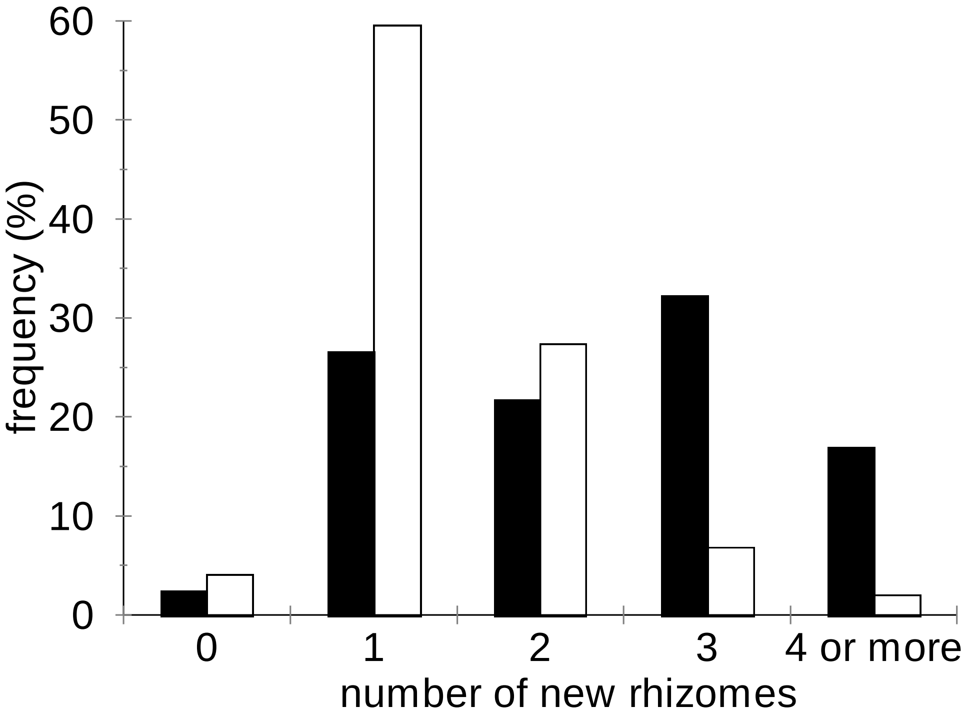


Figure 3: Histogram of the rhizome numbers in dry (filled bar) and wet sites (empty bar)

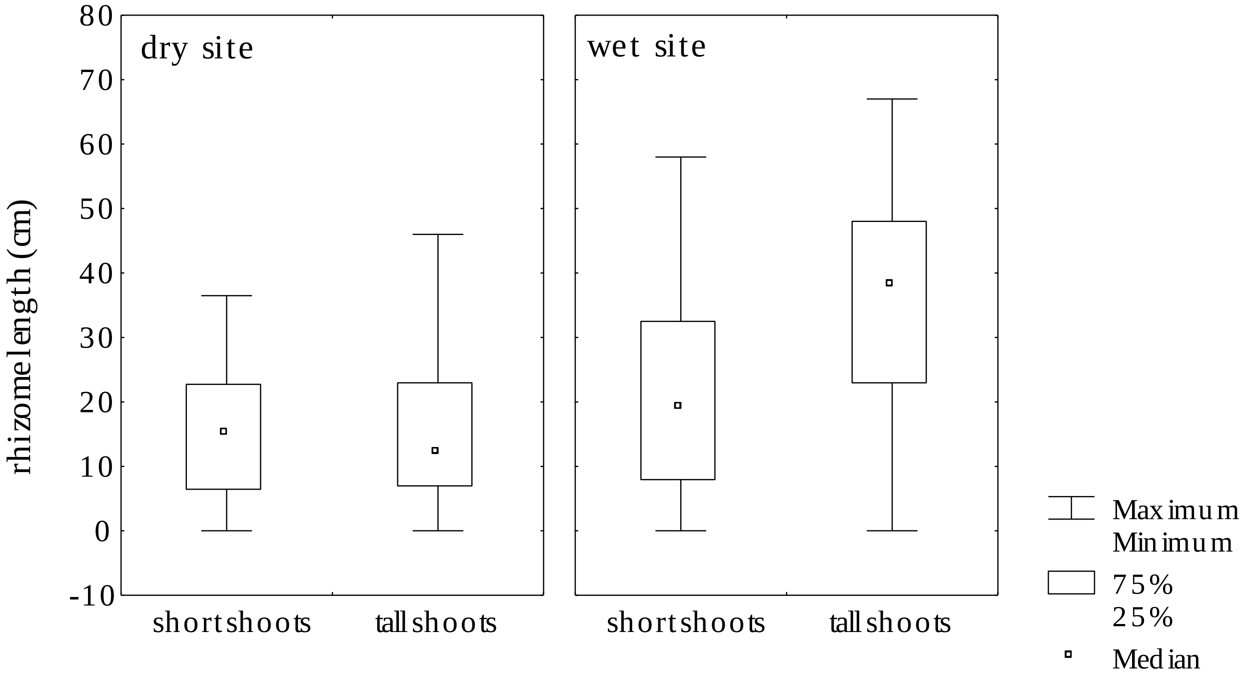
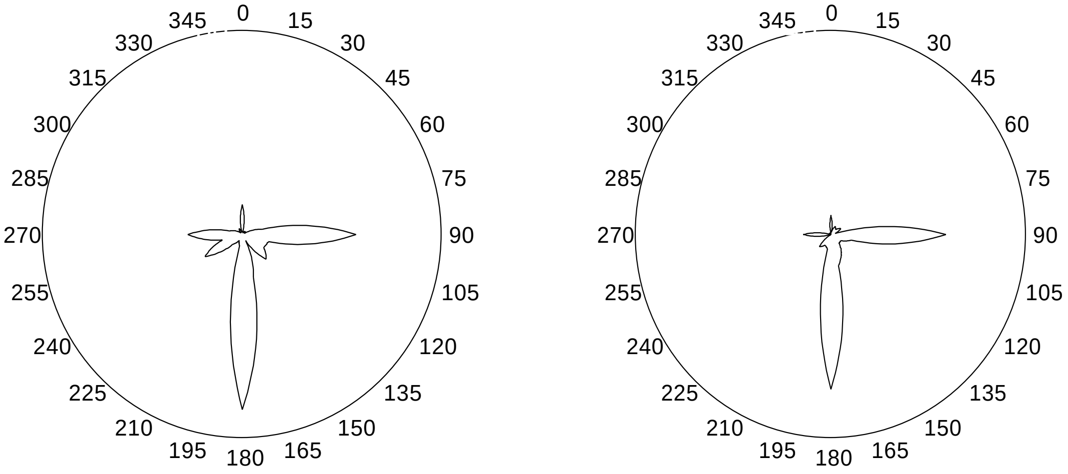
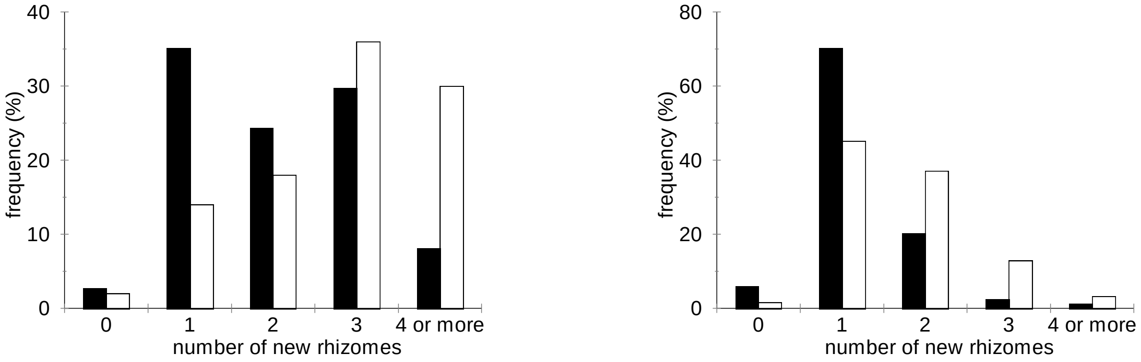


Figure 4: Box and whisker plot of rhizome lengths. Short shoots means shoots shorter, tall shoots means shoots taller than average shoot height in that site. By this division, relatively tall and supressed, relatively short shoots were compared in each site disregarding the average shoot size of sites.



a) dry site b) wet site

Figure 5: Distribution of branching angles (angles beetween old and new rhizomes; see Figure 2)



a) dry site

b) wet site

Figure 6: Histogram of the rhizome number of short (filled bar) and tall shoots (empty bar) in the two sites. Short shoots means shoots shorter, tall shoots means shoots taller than average shoot height in that site. By this division, relatively tall and supressed, relatively short shoots were compared in each site disregarding the average shoot size of sites.