Journal of Ecology 2007
95, 406–413

What youngsters say about adults: seedling roots reflect clonal traits of adult plants

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Summary

1 Grime's theory on plant strategies predicts that the set of traits present in established plants is not correlated with that found in the regenerative stage of the life cycle. We tested this prediction and further investigated whether clonal growth traits, which are found in adult plants but also affect regeneration, are correlated with seedling traits.

2 We characterized seedling root systems by their total length, number of root tips and several architectural parameters (length of exterior and interior root links and two topological indices). These below-ground traits were supplemented by the ratio of leaf area to root length, representing relative investment into photosynthesizing surface. We compared seedling traits with clonal growth traits, adult plant heights, and species positions on gradients of nitrogen and water availability.

3 Plant species with limited horizontal spread by clonal growth exhibited a larger relative investment in photosynthetic area and also developed larger root systems as seedlings.

4 Seedlings of species with taller shoots and those which occur naturally at nutrient-rich sites developed both larger roots and more dichotomously branched root systems (with higher total length and more branches).

5 Taking phylogenetic inertia into account showed that this explained large parts of the variation in seedling traits. Relationships between clonal spread and seedling traits were strengthened by phylogenetic correction.

6 Our study shows that some of the traits of clonal growth affect both the established and the regenerative stages of the life cycle, suggesting that an evolutionary trade-off exists between the ability to spread clonally and performance at the seedling stage. Species not able to escape from less favourable conditions by extensive clonal spread seem to be more able to exploit the location in which they germinate.

Key-words: clonal growth, ecological traits, grassland plant species, lateral spread, leaf area : root length ratio, phylogenetic correction, regenerative stage of life cycle, resource availability, root architecture

Journal of Ecology (2007) **95**, 406–413
doi: 10.1111/j.1365-2745.2007.01218.x

Introduction

As part of his theory of plant strategies, Grime (2001) suggested that intercorrelated traits are found within both the established (mature) and the regenerative (immature) stages of the plant life cycle. He also predicted that there would be no correlation among these two trait groups, as mature and juvenile individuals experience different selective forces, and this lack of coupling has been confirmed in several studies (Shipley *et al*. 1989; Grime *et al*. 1997). Nevertheless, there are traits of adult plants that can affect both the established and the regenerative stages, for example traits related to clonal growth.

Clonal plants, prevalent in many plant communities, including managed grassland of temperate zones (Klimeš *et al*. 1997), are composed of multiple units (ramets) often connected by spacers that we prefer to call clonal growth organs (Klimeš & Klimešová 1999). The modular structure helps adult clonal plants to co-ordinate their foraging for soil resources and light, to share acquired resources among the ramets, or even

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to 'divide the labour' (of resource acquisition) between the ramets (de Kroon & Hutchings 1995; Hutchings & Wijesinghe 1997). However, for many plant species, clonal growth is also an important component of their regenerative strategy, allowing them to create independent offspring by separation of daughter ramets from the mother ramet (Grime 2001). This alternative way of regeneration suggests possible trade-offs between clonal growth and sexual reproduction. Indeed, such trade-offs between clonal growth and reproductive effort have been demonstrated in several species (e.g. Piquot *et al*. 1998; Chaloupecká & Lepš 2004; Weppler *et al*. 2006), as well as trade-offs between clonal growth and seed and dispersal traits (Eriksson 1997; van Kleunen *et al*. 2002). Nevertheless, comparative studies looking for trade-offs between traits at the regeneration (seedling) stage and the traits of clonal growth have been lacking. This paper presents the results of such a study.

Evaluation of functional traits over a wide range of plant species inevitably introduces additional patterns of variation affecting the studied traits. This variation must be controlled for in statistical models to separate it from the patterns under consideration. Specifically, species included in our study occur over a wide range of habitat conditions, in terms of water and nutrient availability, and these gradients do affect plant traits (Fitter 1996; Grime 2001). It can also be expected that the species differ in their general competitive abilities. Therefore, we supplement our data with Ellenberg indicator values (Ellenberg 1988): these values represent species positions along gradients of nutrient and moisture availability and they are therefore partly a consequence of species functional traits. We also included the average maximum plant height at the adult stage as it is an important trait in asymmetric competition for light (Grime 2001) and has been shown to be a good indicator of relative competitive performance (Keddy *et al*. 2002). To make the difference of Ellenberg values from the individual primary traits clear, we refer to them as plant ecological attributes.

Observed variation in ecological traits can be attributed to three major sources: (i) evolutionary constraints (phylogenetic inertia) in which taxa that share part of their evolutionary history possess similar 'blueprints' (Peat & Fitter 1994; Harvey *et al*. 1995) – examples are provided by differences between grasses and dicotyledonous forbs in root system size (Gross *et al*. 1992), root system topology (Taub & Goldberg 1996; Roumet *et al*. 2006) and root foraging precision (Kembel & Cahill 2005); (ii) adaptation of species to average conditions in their environment; and (iii) phenotypic plasticity, the ability of individuals with an identical genotype to develop differently, based on specific conditions during their ontogeny (de Kroon *et al*. 2005; Pigliucci 2005). Although we can suppress the effects of phenotypic plasticity by comparing species grown under standardized conditions, separation of evolutionary inertia from a true adaptation to the environment is impossible, as the evolutionary past defies experimental manipulation. A conservative approach, of discounting all of the variation that could possibly be explained by phylogenetic relatedness of studied species (Harvey *et al*. 1995), has therefore been widely adopted in comparative studies. As a result, the substantial overlap between the variation explainable by the evolutionary past and the variation explainable by environmental properties or other traits is often ignored (Desdevises *et al*. 2003). The least we can do to cope with this issue is critically to compare conclusions made with and without phylogenetic corrections (Kembel & Cahill 2005).

In the present study, we used a large set of grassland plant species to analyse relationships between important traits of the regenerative stage of the plant life cycle (morphological and topological characteristics of seedling root systems and the relative allocation to seedling leaves) and the clonal growth traits and ecological properties of adult plants. In doing so, we addressed the following three questions:

1. Are seedling traits correlated with properties of clonal growth?

2. Do seedling traits correlate with nutrient or water availability in the environment where the species usually occur and with adult above-ground height?

3. How much of the variation in juvenile plant traits can be accounted for by species evolutionary relatedness and to what extent is the relationship between seedling traits and adult plant characteristics affected by evolutionary history?

Materials and methods

STUDY SPECIES AND EXPERIMENTAL DESIGN

Eighty plant species occurring in man-made grasslands of Central Europe, with habitat conditions ranging from wet to dry and nutrient-rich to nutrient-poor, were selected for this study. Seeds were obtained from a local commercial supplier (Planta naturalis, Markvartice u Sobotky, Czech Republic) and sown in Petri dishes filled with heat-sterilized sand. Five- to 7-day-old seedlings were replanted into perlite-filled containers. Each species had four replicates at the start of the experiment. Individual plants were arranged into blocks, consisting of single replicates of each species. The position of individual species within the blocks was completely randomized. Seedlings were grown under benign glasshouse conditions, during June, with natural fluctuations of temperature (15–30 °C) and light conditions. Seedlings were watered as necessary, and supplied with a commercial nutrient solution (Univerzal KH; Explantex Vondruš, Czech Republic; with N : P : K ratio 7.2 : 4.2 : 9.0) immediately after replanting and 2 weeks afterwards, in amounts corresponding to approximately 13 mg of N and 8 mg of P per plant.

Because of mortality during the experiment, 23 species ended up with fewer than two replicates and were

Table 1 Definitions of measured root morphological characteristics used in the paper (see also supplementary Fig. S1 for a graphical presentation of the root attributes)

Characteristic	Definition
EL – exterior link	terminal root section between the meristematic root tip and the nearest branching point
IL – interior link	root section joining other links, i.e. the part of the root between any adjacent branches
μ – magnitude	number of exterior links (i.e. root tips) served by a root
TotL – total length of root	sum of the lengths of all exterior and interior links of the root, expressed in millimetres
p_e – total exterior path length	sum of the number of links in all paths from every exterior link to the base of the root
$\max(p_e)$ – maximal total exterior path length	total exterior path length of an imaginary root of given magnitude if fully herringbone-style branched
$\min(p_e)$ – minimal total exterior path length	total exterior path length of an imaginary root of given magnitude if fully dichotomously branched

excluded from the analysis (the 57 species retained are listed in supplementary Table S1 available online). All seedlings were harvested 3 weeks after transplanting. Complete root systems were gently washed, spread over a glass plate and their images, including above-ground parts, were recorded using a standard flatbed scanner (Astra 600S; UMAX Technologies, Inc., Texas, USA).

MEASURED CHARACTERISTICS

Topological properties of complete root systems were quantified from the recorded images using RootArch software (P. Šmilauer, unpublished). We evaluated several root morphological characteristics for each root system: ELL, average length of exterior links; ILL, average length of interior links; μ, magnitude of the root system; TotL, total length of the root system; $L : R$, leaf area to root length ratio, and two topological indexes $\log(p_e) : \log(\mu)$ and DBI (see Table 1 and below for definition of parameters: further details are available in Fitter (1996) and in supplementary Fig. S1). The dichotomous branching index (DBI, Šmilauerová & Šmilauer 2002) is calculated for a particular root system, using its total exterior path length, p_e, as

$$\mathrm{DBI} = [p_e - \min(p_e)] : [\max(p_e) - \min(p_e)].$$

Both topological indices place a root system on a scale whose extreme points represent a dichotomously branched vs. a 'herringbone' branched root system. In the latter case, there are only first-order lateral roots, because only the main axis branches (see supplementary Fig. S1). The DBI characteristic has the advantage of standardizing the range of values between 0 (dichotomous branching) and 1 (herringbone branching).

Leaf area was estimated from scanned images of individual seedlings. The ratio of leaf area to total root length was calculated separately for each seedling. Hereafter, the measured seedling characteristics (including the $L : R$ ratio) are referred to as the root traits.

ADULT PLANT CHARACTERISTICS

Traits of adult plants (characteristics of clonal growth and average height, H, in their natural habitats) and their ecological attributes (Ellenberg indicator values for moisture, F, and nitrogen, N) were compiled from the literature for each species (Ellenberg 1988; Adler *et al*. 1994; Klimešová & Klimeš 2006). The following characteristics of clonal growth organs (CGO) were used, all treated as comprising discrete categories: developmental origin of CGO (stem vs. root), CGO developmental mode (initial and final positions of CGO with respect to the soil surface), and extent of annual lateral spread (< 1 cm, 1–25 cm, 25 cm). Individual categories of each of the clonal traits were represented as dummy variables (see Legendre & Legendre 1998, p. 46) in the data matrix. For a plant species capable of developing several types of CGO, we used all the trait states implied by different CGO types, weighted by the relative frequency of their records in the database (Klimešová & Klimeš 2006). As an example, there were two records of *Galium pumilum* indicating stem origin of its CGO, and one record indicating root origin. The two dummy variables representing CGO developmental origin (stem vs. root) therefore had values of 0.67 and 0.33, respectively. Species without clonal behaviour (4 of 57) were omitted from the clonal growth analyses.

Species with an 'indifferent behaviour' (i.e. with a wide tolerance to soil moisture or nitrogen availability based on Ellenberg indicator values) were omitted. To test whether such omissions introduced any bias into the analyses, hypotheses of no difference in root properties between the indifferent species and the species with narrower amplitude were also tested.

Average maximum height of adult individuals was calculated as a mean value from the range given by Adler *et al*. (1994).

DATA ANALYSIS

Relationships between seedling traits and the adult plant characteristics were evaluated using linear models fitted for each predictor (adult plant characteristic) and each response variable (seedling trait) separately. Type I errors were estimated using non-parametric Monte Carlo permutation tests, based on the F statistic, with 999 random permutations. When phylogenetic corrections were used, individual linear models also

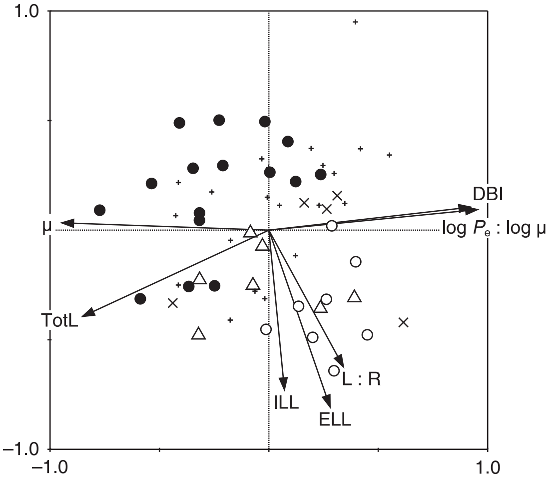

Fig. 1 Ordination diagram with the first two PCA axes (explaining 76% of the total variance in a standardized data matrix). Arrows point in the direction of increasing expected values of corresponding root traits, symbols represent individual plant species, and the type of symbol codes species membership in the four most frequent families: Poaceae, filled circles; Asteraceae, empty circles; Fabaceae, triangles; Rosaceae, crosses; other families, plus symbols. Relative values of individual species for a trait can be deduced by a perpendicular projection of the species symbols onto the trait arrow; the Pearson correlation coefficient is approximated by the cosine of the angle between the arrows of two traits being compared (ter Braak & Šmilauer 2002).

included covariates, representing phylogenetic relatedness of individual species (see below for further explanation). Families of models testing similar hypotheses were identified as those with identical predictors and related response variables, i.e. DBI and log(p_e) : log(μ) for root topology, μ and TotL for root system size, and ELL and ILL for root link dimensions. Family-wise error rate was controlled for by Bonferroni correction of significance values.

Both the correlations within the group of seedling traits and the correlations within the group of adult plant characteristics were examined. Correlations among root traits were summarized using principal component analysis (PCA; see Legendre & Legendre 1998) calculated from the correlation matrix; the ordination diagram was created with scaling focused on correlation between the variables (ter Braak & Šmilauer 2002). Major families of grassland plants are distinguished in the diagram to visualize root trait differences related to phylogenetic inertia. Dependencies between adult plant characteristics were tested by linear models and are presented for the characteristics that were found to be significant predictors of seedling traits.

The method of Diniz-Filho *et al.* (1998), as modified by Desdevises *et al.* (2003), was used in tests including phylogenetic corrections. In this method, the variation explained by the phylogenetic relatedness of species is removed from the model, using species coordinates on selected axes of a principal coordinate analysis (PCoA) calculated from a patristic distance matrix corresponding to a phylogenetic tree. This tree was created for our set of species by starting from the family-level tree published at the website of the Angiosperm Phylogeny Group (APG 2003), with the estimates of divergence time and structural details at the subfamily level obtained from a wide range of publications, with the most important being Stevens (2001), Bremer *et al.* (2002), Eriksson *et al.* (2003) and Judd & Olmstead (2004). Selection of principal coordinates was based on a stepwise selection procedure, in which all root traits served as response variables (redundancy analysis – RDA; see Legendre & Legendre 1998). Selected principal coordinates, which were used as covariates during tests including phylogenetic correction, were also used as predictors for individual root traits to estimate the amount of variation in the trait values explained by species phylogeny (Desdevises *et al.* 2003). Particular attention was paid to the difference between grasses and dicots, as it represents the principal coordinate with the largest explanatory power for seedling traits.

All statistical methods were applied using CANOCO for Windows 4.53 (ter Braak & Šmilauer 2002), including the estimation of linear models (performed using RDA with a single response variable).

Results

MAIN PATTERNS IN SEEDLING TRAITS

We evaluated root systems of 188 seedlings belonging to 57 species. The average values of measured traits and adult plant characteristics for individual species are given in supplementary Table S1. Correlations between individual seedling traits can be seen from the PCA ordination biplot (Fig. 1). The first (horizontal) axis represents a gradient of change in the architectural parameters DBI and log(p_e) : log(μ), increasing from left to right (roots of species at the right side have more 'herringbone'-like branching), and also a gradient of root system magnitude (μ) increasing in the opposite direction. The second (vertical) axis is correlated with a change in average length of interior and exterior links (ILL and ELL), increasing from top to bottom. The most apparent differences can be seen between grasses (filled circles) and dicots (other types of symbols), mainly in the average length of exterior links, the magnitude of the root system and the $L : R$ ratio values (see Table 2). Nevertheless, differences among grasses and dicots were significant for all root traits, except for total root length. The difference in the average length of interior links was borderline significant ($P = 0.074$).

Table 2 also gives the fraction of variation in the measured root traits that can be accounted for by evolutionary history. The largest amount of variation was explained in exterior link length (60.6%) and root system magnitude (44.4%). Stepwise selection of principal coordinates, representing components of phylogenetic relatedness that significantly explain differences in root

Table 2 Test results for the difference of individual root traits between grasses (Gr) and dicots (Di) (second and third columns) and the percentage of trait variation explained by phylogenetic relatedness between the species. The *P* (*F*) column shows Type I error probability estimates (after Bonferroni correction, where appropriate), together with the corresponding *F* statistic from the permutation test. See Table 1 and the Methods section for acronym definitions

	Grasses × dicots		Evolutionary history (% explained)
Root trait	Response	P ($F_{1,55}$)	
ILL	Gr < Di	0.074 (4.83)	28.9
ELL	Gr < Di	0.001 (16.38)	60.6
μ	Gr > Di	0.001 (14.98)	44.4
TotL	(Gr > Di)	NS (3.75)	27.8
L : *R*	Gr < Di	0.001 (11.97)	30.7
log(p_e) : log(μ)	Gr < Di	0.012 (9.04)	36.0
DBI	Gr < Di	0.025 (6.82)	31.7

properties, indicated that five axes should be considered and these explained 37.9% of the total variation in seedling root traits. The most important axis separated grasses from dicotyledoneous species.

RELATIONSHIPS BETWEEN SEEDLING TRAITS AND CLONAL TRAITS OF ADULT PLANTS

Species with more limited lateral spread had seedlings with larger root systems (TotL) and a higher relative investment in photosynthetic area, i.e. a higher *L* : *R* ratio (Table 3). The latter effect manifested itself both in phylogeny-corrected and ahistorical (uncorrected) tests ($P = 0.003$ and 0.014, respectively), while the response of total root length could be seen only when a phylogenetic correction was applied ($P = 0.050$). Root topology, *L* : *R* ratio and the number of root tips differed weakly between species with root vs. stem origin of clonal growth organs (Table 3). These relationships disappeared, however, when phylogenetic correction was applied. No significant relationships (with $P < 0.1$) were found between mode of clonal growth (above-ground vs. below-ground origin and growth of CGO) and individual seedling traits.

RELATIONSHIPS BETWEEN SEEDLING TRAITS AND ADULT PLANT HEIGHT AND ECOLOGICAL ATTRIBUTES

Both the maximum height of adult plants (*H*) and the position of species on the gradient of nitrogen availability (*N*) were reflected in a very similar way in measured seedling traits (Table 3). Thus, seedlings of species from nitrogen-rich stands and/or of tall species had more dichotomously branched root systems with greater total length and magnitude, but did not differ in the other root traits (branching density, as reflected in ELL and ILL values, or relative investment to leaves, with the exception of a significant relationship between *L* : *R* ratio and the *N* variable after phylogenetic correction). The similarity in response of seedling traits to *N* and to *H* can be explained by the positive, significant relationship between *H* and *N* ($P = 5.9 \times 10^{-6}$ or 0.001 after phylogenetic correction).

No significant relationship was found ($P > 0.1$) between species indicator values for moisture conditions and any of the seedling traits. Similarly, we found no significant difference between those plant species indifferent to nitrogen availability or moisture gradients and those with a specific position on these gradients, for any of the root traits.

Discussion

CLONAL TRAITS OF ADULT PLANTS

Clonal characteristics of adult plants are important for the effective placement of their ramets into locations appropriate for acquisition of water, nutrients and/or

Table 3 Results of partial tests of relationships between individual root traits of seedlings (in rows) and adult plant characteristics. AH headed columns refer to ahistorical comparisons (i.e without phylogenetic corrections), while PC headed columns refer to models with a correction for phylogenetic relatedness (Desdevises *et al*. 2003). *N* refers to Ellenberg indicator value for nitrogen, *H* to average height of adult plants. Individual cells show Type I error probability estimates (adjusted by Bonferroni correction within test families) and related *F* statistic values (in parentheses) of individual permutation tests, or NS when adjusted $P \geq 0.10$. Degrees of freedom for *F* statistics are (1,55) for *N* (AH), (1,51) for other ahistorical tests, (1,50) for *N* (PC), and (1,46) for other phylogeny-corrected tests. Arrows indicate the effect direction for a significant relationship (upward pointing arrow implies increase of the root trait value with increasing value of the predictor; for CGO origin column, an upward pointing arrow implies larger root trait values for the root origin of CGO). See Table 1 and Methods for trait definitions

	N		*H*		CGO spread		CGO origin	
Root trait	AH	PC	AH	PC	AH	PC	AH	PC
ILL	NS	NS	NS	NS	NS	NS	NS	NS
ELL	NS	NS	NS	NS	NS	NS	NS	NS
μ	↑0.022 (7.73)	0.030 (6.30)	↑0.026 (6.57)	NS	NS	NS	↓0.088 (4.29)	NS
TotL	↑0.012 (8.26)	0.020 (7.97)	↑0.070 (4.72)	0.094 (3.96)	↓NS	0.050 (9.89)	NS	NS
L : *R*	↑NS	0.039 (4.70)	NS	NS	↓0.014 (13.91)	0.003 (16.15)	↑0.034 (4.77)	NS
log(p_e) : log(μ)	↓0.004 (13.61)	0.002 (17.04)	↓0.016 (8.06)	0.046 (5.95)	NS	NS	↑0.052 (5.69)	NS
DBI	↓0.012 (8.79)	0.006 (11.88)	↓0.014 (8.15)	0.042 (5.93)	NS	NS	↑0.048 (5.9)	NS

light (de Kroon & Hutchings 1995), but also for general dispersal within a community and for plant regeneration after disturbance events. Based on the results of this study, seedlings of species with fast lateral spread in adult stages are likely to have limited root size and a low relative investment in leaves (small $L : R$ ratio). There are few species in our dataset with the ability for extensive lateral spread, however, so a more appropriate interpretation is probably that seedlings of species with limited clonal growth exhibit a strategy of occupying space quickly, both above- and below-ground. This is done by developing long, branched roots and investing more in leaf area.

It is interesting to contrast our conclusion with the results of Shipley *et al.* (1989), who compared seedling and adult traits of emergent macrophytes. They found that two sets of traits, representing plant regeneration strategy and establishment strategy, were uncorrelated, in accordance with Grime's model of plant strategies (Grime 2001). This disagreement can be explained by a different set of traits chosen in the two studies. Although the traits used by Shipley *et al.* (1989) for adult plants were at least partly similar to ours (plant height and clonal growth properties), characteristics of regeneration strategy were very different (seed weight, germination rates under different conditions, seedling relative growth rate).

The negative relationship between root system size and relative leaf area on the one side and the extent of lateral vegetative spread on the other signifies a trade-off between seedling competitive ability and the ability of adult plants both to locate part of the clonal system into more favourable microsites and to place their non-generative offspring (ramets separated from their mother plant) into the same kind of microsites. Because the same seedling traits are also correlated to species N values and, more weakly, to H values (see Table 3), we might suspect that the former finding may just be a consequence of a possible negative correlation between adult plant height and a species' ability to spread laterally. Such a negative correlation would support the suggestion of Aarssen *et al.* (2006) that clonal growth limits adult plant size. However, no significant relationships were found between the extent of lateral spread of adult plants and the H and N values ($P > 0.1$ for both tests). Therefore, it seems likely that this trade-off reflects evolutionary pressure against sexual reproduction in plant species with an effective means of clonal spread (Eriksson 1997).

Differences between species with clonal growth organs originating from roots or stems, as seen in the length and magnitude of the seedling root system, as well as the type of branching disappeared once phylogenetic relatedness was taken into account. This, together with the fact that these root traits are identical to those that distinguished grasses from dicots (see Table 2), indicates that the relationship is an artefact resulting from the inability of grasses to create root-derived clonal growth organs (Klimeš *et al.* 1997). Although we found several evolutionary dichotomies to be reflected in seedling root traits (such as the difference between rosid and asterid lineages), the difference between grasses and dicotyledonous species emerges as the most important one, as found in other comparative studies (e.g. Kembel & Cahill 2005; Roumet *et al.* 2006).

SPECIES FROM RICH VS. POOR HABITATS

Fitter (Fitter 1991; Fitter *et al.* 1991) predicted that a herringbone type of root branching should be more efficient for slow-growing species occurring in resource-poor habitats, while annuals and other species from nutrient-rich habitats should produce more dichotomously branched root systems. These predictions are supported by our results (Table 3), obtained at the early stages of seedling growth under standardized conditions. Seedlings of species from habitats with higher nitrogen availability had longer roots and more root tips than species from habitats with lower nitrogen availability.

Differences in root length and branching intensity can, however, merely be a consequence of a higher growth rate of species from nutrient-rich habitats (Grime 1994; Fransen *et al.* 1999), which are able to produce root biomass more quickly and branch earlier than the more slowly growing species. Our experimental approach, in which seedlings of different plant species were harvested at the same time, does not allow us to separate the effect of growth rate from time-independent differences in the morphological traits of root systems. Nevertheless, our finding that the relationship between seedling traits and the nutrient status of their natural habitats is essentially identical to the relationship between seedling traits and species competitiveness (approximated by average maximum height) does suggest that this is yet another manifestation of one of the primary axes of species life-history evolution (Grime 2001). This is further supported by the positive correlation between N and H predictors. Therefore, interspecies differences in growth rates must operate here, too.

Surprisingly, the soil moisture preference of the studied species showed no relationship to any of the seedling root traits. This contradicts the findings of Nicotra *et al.* (2002); however, Nicotra *et al.* used several different root traits (such as root anatomy characteristics and specific root length) and their set included woody as well as herbaceous species.

Conclusions

Despite extensive phylogenetic inertia in the seedling root traits studied, several important links between these traits and adult plant characteristics were found after removing effects of phylogenetic relatedness.

Besides the relationship to the gradient of habitat productivity, represented in our study by species occurrence in habitats with different nitrogen availability and by different adult plant heights (as a proxy of species competitiveness), a surprising relationship was found between the traits important at the regenerative stage of the life cycle (root system size and relative investment in photosynthetic area) and the scale of clonal growth of adult plants. We suggest that this relationship reflects a trade-off between the ability of adult plants to place individual ramets effectively in suitable 'feeding locations' by means of clonal growth and the potential competitive performance of seedlings. Plant species with the ability to 'escape' less favourable locations and place their vegetative offspring in favourable microsites do not exploit so vigorously the location in which they germinated. This is a novel finding that we hope will prompt new research in this area. It would be interesting to repeat such a comparative study with the focus on selecting species in a balanced manner with respect to both the extent of clonal spread and the habitat type, and not limiting the choice just to grasslands, as we did. Another promising direction is to compare clonal growth traits of adult plants with the performance of seedlings in controlled environments of varying spatial heterogeneity in soil and/or light resources.

Acknowledgements

We thank Jitka Klimešová for providing information about plant species clonality from the CLOPLA database, Milan Štech for the outline of phylogenetic relationships among studied taxa, and Jonathan Titus, Sylva Pecháčková, Peter Alpert and two anonymous referees for important suggestions on an earlier draft of the manuscript. We also thank Jonathan Titus and Keith Edwards for language revisions. This work was funded by a grant from the Czech Ministry of Education, MSM-6007665801.

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*Received 16 October 2006;
accepted 13 December 2006
Handling Editor: Peter Alpert*

Supplementary material

The following supplementary material is available for this article:

Table S1 List of studied species and their trait values

Fig. S1 Root architectural parameters.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2745.2007.01218.x