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ON PLASTIC AND NON-PLASTIC VARIATION IN CLONAL PLANT MORPHOLOGY AND ITS ECOLOGICAL SIGNIFICANCE

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Abstract: Morphological plasticity in clonal plants has received wide attention because localized plastic changes in spacer length, branching intensity and branching angle may enable clonal plants to place ramets selectively in the more favourable microhabitats within a heterogeneous environment. These responses have been interpreted in terms of foraging behaviour.

Studies of morphological plasticity in clonal plants are usually carried out with one or two genotypes of a species, or with material of unknown genetic origin. Based on the concept of phenotypic plasticity, it is argued that such studies do not reveal whether plasticity in a population can be modified by natural selection. In addition, responses are often evaluated at two environmental conditions only, which may underestimate plasticity. Hence, our information on the ecological and evolutionary significance of morphological plasticity in clonal plants is still very incomplete.

Two examples are given to show that stolon internode and rhizome lengths may vary considerably within an individual plant. Only a minor part of this variation may be plastic, i.e. the variation is hardly changed by the environmental conditions to which the plants are subjected. Hence, non-plastic variation in clonal morphology may exceed the degree of morphological plasticity. The non-plastic variation seems to originate from species-specific patterns of stolon and rhizome development.

Marked non-plastic variation may obscure the effects of morphological plasticity on the placement pattern of ramets in the field, suggesting that plasticity in clonal morphology may not be very effective in terms of foraging for favourable patches. Possible reasons for the low levels of plasticity of clonal spacers are discussed.

INTRODUCTION

Clonal architectures may be conspicuously different between species (BELL & TOMLINSON 1980, LEAKEY 1981, BELL 1984). However, the growth form parameters of species are not fixed. As early as 1909 WARMING appreciated the large plasticity of plant morphological characters in response to environmental conditions. Within the contemporary ecological literature, COOK (1983, 1985) was among the first to emphasize the importance of morphological plasticity in clonal plants. A well-known example of morphological plasticity is shown by the stoloniferous herb *Glechoma hederacea*. This species branches sparsely and forms relatively long stolon internodes under conditions of low light or low nutrient supply, while under more favourable conditions a more compact growth form with frequent branching and shorter internodes is produced (SLADE & HUTCHINGS 1987a,b). These responses have drawn attention because of their potential benefits in a spatially heterogeneous environment (e.g., SALZMAN 1985, SLADE & HUTCHINGS 1987a,b, SUTHERLAND & STILLMAN 1988). Natural habitats are usually inherently patchy, consisting of microhabitats with a high supply of water, nutrients or light that are interspersed by patches with a lower supply of these resources (SVENSSON & CALLAGHAN 1988, HOOK et al. 1991, KELLY & CANHAM 1992, JACKSON & CALDWELL 1993a,b). It has been suggested that plasticity in growth form may increase the probability that ramets are placed in the more favourable microhabitats within such environments. Plasticity in clonal plant morphology is thus interpreted as a behavioural ("foraging") phenomenon, allowing the plant to search its environment for patchily distributed resources (HUTCHINGS 1988, HUTCHINGS & MOGIE 1990, SUTHERLAND 1990, DE KROON & SCHIEVING 1990, DE KROON & VAN GROENENDAEL 1990, OBORNY 1991).

The notion that clonal spacers (rhizomes, stolons) serve as structures that forage selectively for favourable microhabitats within the environment, has recently become the subject of debate. HUTCHINGS & DE KROON (1994), reviewing the literature on morphological plasticity in plants, tentatively concluded that the degree of morphological plasticity exhibited by clonal spacers is generally much smaller than the morphological plasticity of orthotropic stems and roots of individual ramets. Moreover, several studies have demonstrated that clonal spacers of some species do not show significant morphological responses at all, or respond in ways that do not accord with the model of selective foraging. HUTCHINGS & DE KROON (1994) suggested that root and (orthotropic) shoot foraging may be more effective in exploiting favourable patches than the morphological plasticity of the stolons and rhizomes of many species. In contrast to earlier propositions, clonal spacers in some species may enable the plant to spread its ramets across the environment in a relatively unresponsive way, while the local morphological responses by the shoots and roots of individual ramets allow for selective foraging.

However, in a survey of the morphological responses of stolons and rhizomes, DE KROON & HUTCHINGS (in press) found that most stoloniferous species are consistent in producing shorter stolon internodes and branching more intensively at higher light levels. Recent simulation studies suggest that responses of the magnitude exhibited by the stolons may result in a significantly higher concentration of ramets in the better microenvironment (OBORNY 1994) or in a significant higher displacement from a point of origin in habitat of lower quality (CAIN 1994). However, the foraging efficiencies of clonal spacers have not been compared to those of roots and shoots and the ecological and evolutionary significance of morphological plasticity of clonal spacers remains an unsolved issue up to date.

In this paper we contribute to the debate by a reconsideration of the ways in which morphological plasticity is measured in studies of clonal plants and by contrasting plastic versus non-plastic variation in morphological characters. Firstly, we define and delimit the concept of morphological plasticity in plants. Secondly, we consider some of the problems that arise in measuring morphological plasticity and in interpreting and comparing data in the literature. Thirdly, examples of non-plastic variation in morphological characters of clonal plants are given, i.e. variation that is not modified by the environmental conditions to which the plants are subjected. We conclude with a discussion of the implications of these issues for the ecological and evolutionary significance of morphological plasticity of clonal plants in heterogeneous habitats.

WHAT IS MORPHOLOGICAL PLASTICITY?

According to BRADSHAW in his seminal 1965 review paper, "plasticity is shown by a genotype when its expression is able to be altered by environmental influences. The change that occurs can be termed the response. Since all changes in the characters of an organism which are not genetic are environmental, plasticity is applicable to all intragenotypic variability". In recent years, plant ecologists have increasingly used plant "behaviour" as an alternative term to phenotypic plasticity (SILVERTOWN & GORDON 1989). Note that the definition does not specify the nature of the relationship between a character and an environmental variable (increasing or decreasing, linear or non-linear) or the magnitude of the response. In addition it is important to realize that "the concept of plasticity does not have any implications concerning the adaptive value of the changes occurring, although many types of plasticity may have important adaptive effects" (BRADSHAW 1965).

"Plasticity in the sense defined here does not include variation which is directly genetic in origin", but "the plasticity of a character is an independent property of that character and is under its own specific genetic control" (BRADSHAW 1965). While, by definition, plastic variation is environmentally induced, the direction and magnitude of the response is genetically determined. However, there is considerable controversy about the genetic mechanism underlying phenotypic plasticity (see the recent discussion in VIA 1993a,b, SCHLICHTING & PIGLIUCCI 1993, SCHEINER 1993a,b). One view, adhered to by BRADSHAW (1965), considers plasticity as a character in its own right and under its own genetic control, separately of the mean value of the character. According to another opinion plasticity is evolved as a byproduct of natural selection on the phenotypic value of the character in each of the environments.

Phenotypic plasticity is typically analyzed by "norm of reaction" diagrams (SCHLICHTING 1986, VIA 1987, 1993a). Such diagrams compare the mean phenotypic values expressed by individuals of a single genotype (or closely related genotypes) under two or more environmental conditions as shown graphically in Fig. 1. In this representation, the slopes measure the extent of plasticity of the genotypes while the intercepts are the genotypic mean values of the character in the two environments. In the analysis of norms of reaction diagrams we should distinguish between the plasticity of a genotype and the mean plasticity at the population level (VIA 1993a). A population may consist of genotypes that differ in mean phenotypic value of a character which is non-plastic (Fig. 1A), or may consist of genotypes that are all plastic but to the same degree (Fig. 1B). In these cases there is no genetic variation in phenotypic plasticity, i.e. the norms of reaction are parallel. In Figs. 1C and 1D the slopes vary among genotypes: there is genetic variation in the norm of reaction, or, in other words, the genotype by environment (G x E) interaction is significant. Note that a population may exhibit significant plasticity but no genetic variation in plasticity (Fig. 1B), or exhibit a significant GxE interaction while the mean phenotypic value is the same for all genotypes and the mean norm of reaction is zero (Fig. 1C). If all genotypes in a population exhibit exactly the same level of morphological plasticity, as in Fig. 1B, evolution towards a new

	A	B	C	D
Plasticity of a genotype	Absent	Present	Present	Present
Mean plasticity of population	Absent	Present	Absent	Present
Genetic variation in average environment	Large	Large	Small	Small
Variation in plasticity	Absent	Absent	Present	Present

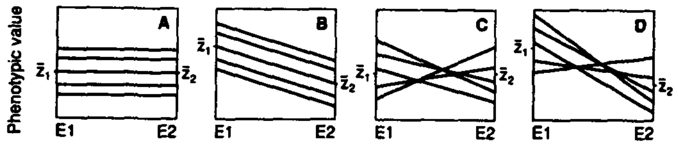

Fig. 1. Graphical representation of the norms of reaction of a character for a population consisting of five genotypes. The mean value of the character expressed by a given genotype in Environment 1 (E1) is plotted on the left vertical axis, the mean value in Environment 2 (E2) is plotted on the right axis. The slopes of the line connecting these genotypic means denote the phenotypic response of each genotype to the change in environment. $\bar{z}_1$ and $\bar{z}_2$ are the population means of the characters expressed by the five genotypes in E1 and E2, respectively. A to D represent four hypothetical situations for each of which the following characteristics are given below: the presence or absence of plasticity of each of the genotypes, the presence or absence of mean plasticity in the population (i.e. $\bar{z}_1 - \bar{z}_2$), the degree of genetic variation in an "average" environment, the presence or absence of genetic variation in plasticity (i.e. genotype by environment interaction). (Modified after VIA 1987 and VIA 1993a)

norm of reaction in response to natural selection will not be possible (VIA 1987). However, such plasticity may be of ecological importance by contributing to the fitness of all individuals in the population compared, for example, to species with a response such as in Fig. 1A in the same environment.

The definition of phenotypic plasticity emphasizes that a plastic change in the expression of a character should be a response to a change in **environmental** conditions. BRADSHAW (1965) noted that "there is an apparent plasticity which is not true plasticity, since its modification occurs independently of the environment. The phenotypic variation is in fact fixed, being endogenous and not exogenous". Bradshaw gives examples of ontogenetic differentiation in plants, such as heteroblastic leaf development, that creates intragenotypic variation in morphology but that does not have an environmental cause. BULL (1987) and VIA (1993a) contrast phenotypic plasticity with "developmental noise" or instability, non-plastic phenotypic variation caused for example by "errors" of development. Responses to random environmental noise are also considered as examples of non-plastic variation although, strictly speaking, they should be qualified as plasticity. Substantial non-plastic variation may obscure genetic differences in plasticity. In Fig. 1 the mean norm of reaction of a population will be estimated by exposing replicate plants of the same genotypes to the same set of environmental conditions. If genotypes show a large amount of phenotypic variation **within** each of the environments, the situations depicted in Figs. 1C and 1D may be statistically indistinguishable from Figs. 1A and 1B, respectively.

MEASURING MORPHOLOGICAL PLASTICITY IN CLONAL PLANTS

We discuss two problems with measuring morphological responses in plants and interpreting the results. The first caveat is related to the genetic identity of the plant material that is used in experiments and the second to the levels of resource availability applied. Finally, studies on morphological plasticity in *Trifolium repens* are discussed to illustrate the problems that may appear when results from different experiments are compared.

The genetic identity of the plant material

In principle, each genotype has its own phenotypic response (Fig. 1) and the mean morphological plasticity of a population could be measured as the average norm of reaction of a representative number of genotypes from the population. This, however, is not common practice in studies of morphological plasticity in clonal plants. Typically, clonal replicates of only one (SLADE & HUTCHINGS 1987a,b, THOMPSON & HARPER 1988, EVANS 1992) or two (SOLANGAARACHCHI & HARPER 1987, THOMPSON 1993) genotypes are examined, or, alternatively, the genetic identity of the material is unknown (MITCHELL & WOODWARD 1988, DE KROON & KNOPS 1990, SCHMID & BAZZAZ 1992). Very few studies on morphological plasticity in clonal plants can be found within the ecological literature that have used a larger number of different genotypes (LOVETT DOUST 1987, DONG 1993).

Both options with respect to the origin of the material have their drawbacks. If only one or two genotypes are examined, measurements will give a precise estimate of the plasticity of these genotypes, but not an estimate of the mean plasticity of the entire population or the species. It is possible that accidentally an atypical genotype may be selected for the study. If material of unknown genetic origin is used the mean morphological plasticity of the population can be estimated accurately (VIA 1993a), if also plants are randomly chosen from a population and the replication per treatment is sufficiently large. However, if the genotype by environment interaction is large compared to the mean phenotypic response (as in Fig. 1D), the phenotypic plasticity present in the population will be underestimated.

It should be stressed that neither of these two common choices with respect to the genetic identity of the experimental plants in studies of morphological plasticity gives information about the degree of genetic variation in response. Hence, inferences from the results of these studies on the adaptive significance of morphological plasticity should be treated with caution.

The few studies carried out with clonal plants that did analyze genotype by environment interactions show that genotypes may differ in the degree of morphological plasticity (SOLANGAARACHCHI & HARPER 1987, CARADUS & CHAPMAN 1991, GEBER et al. 1992, CARADUS et al. 1993). The studies by CARADUS and co-workers with large numbers of genotypes from several commercial varieties of *Trifolium repens* are particularly noteworthy. Recently, SCHMITT & WULFF (1993) reviewed the morphological responses of shoot internode length to light quality and proposed a research programme on disruptive phenotypic selection of plant height growth at different plant densities (see also SKÁLOVÁ & KRAHULEC 1992, SCHMID & WEINER 1993, THOMAS & BAZZAZ 1993). Such a programme could be made applicable to investigations of morphological plasticity in clonal plants.

Levels of resource availability

The morphological responses measured in an experiment will depend on the actual levels of resource availability at which the responses are compared. Let us consider the two most important morphological characters in clonal plants, internode length of rhizomes or stolons and branching frequency. At very low resource availabilities, at which little growth is achieved, growth and plasticity will be closely coupled. At such levels, an increase in resource availability is likely to increase the growth of the plant by an increase in the rate of module production (i.e. by increased clonal branching) as well as by an increase in the size of individual modules (including larger internode length). At higher resource availabilities, branching intensity is likely to remain positively related to growth. Indeed, many clonal species realize a significant part of their growth through the production of new modules (CAIN 1994, HUTCHINGS & DE KROON 1994, DE KROON & HUTCHINGS in press). Plasticity in internode length, by contrast, may be decoupled from growth and internodes may become shorter as resource levels increase still further.

As a result, over a sufficiently wide range of resource availabilities, the responses of internode length and other morphological characters may describe an optimum curve. This has been demonstrated by THOMPSON (1993) for the responses of stolon internode length and petiole length of *Trifolium repens* over a gradient of Photosynthetic Active Radiation (Fig. 2). At deep shade in forest understorey, lengths increased with increasing light levels. At still higher PAR corresponding more with full sunlight, however, internode and petiole lengths were shorter. In contrast, clonal branching intensity progressively increased over the whole trajectory of PAR (THOMPSON 1993).

This notion of optimal response curves has important implications for the way in which to measure morphological plasticity. Common practice in studies of morphological plasticity is to subject plants to only two levels of resource availability. From Fig. 2 we can readily see that the changes in stolon internode or petiole length that are recorded will depend on the actual levels of resource availability that are supplied. Even if the difference in resource supply is sufficiently large, no significant change in length may be measured if the responses are assessed at opposite sides of the resource level at which maximal length is realized. This observation calls for experiments in which multiple resource levels are investigated over a sufficiently wide range of conditions.

An example: *Trifolium repens*

Results on morphological plasticity of *Trifolium repens* illustrate well how comparisons between studies may be hampered if different genetic material is used and different resource levels are applied.

SOLANGAARACHCHI & HARPER (1987) and THOMPSON & HARPER (1988) found that stolon internodes of *T. repens* under "high" light were 2-3 times longer than under simulated canopy shade. In these greenhouse studies, relatively low levels of Photosynthetic Active Radiation were applied both in the shading **and** in the "full light" treatments. The responses were assessed at the left part of the PAR trajectory in Fig. 2, and can thus be reconciled with the field study by THOMPSON (1993).

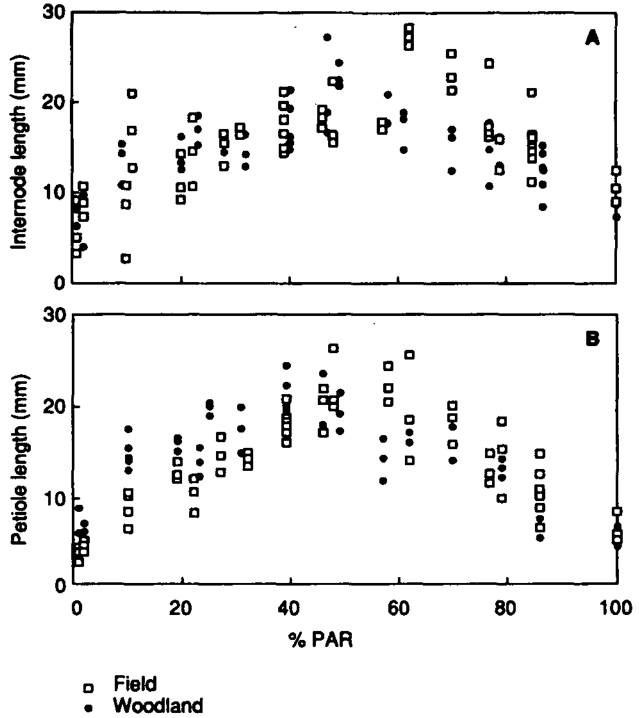

Fig. 2. (A) Mean stolon internode length and (B) mean petiole length of *Trifolium repens* subjected to a range of levels of photosynthetic active radiation (PAR) transmitted by natural canopies in the field. Two genotypes were used, one from a shaded edge ("woodland", open squares), the other from the centre ("field", closed circles) of a grazed pasture. Redrawn from THOMPSON (1993).

CARADUS & CHAPMAN (1991) grew genotypes of two commercial cultivars of *T. repens* in a common garden under full sunlight and under shade cloth providing 50% of full sunlight. Opposite to what would be expected on the basis of the results of THOMPSON (1993; see Fig. 2A), stolon internode lengths were a significant 15% **longer** in the unshaded compared to the shaded treatment. THOMPSON (1993) used two genotypes from an old grazed pasture in her experiment, and the differences in response between the studies may have their cause in the genetic differences of the material. It is also possible that auxiliary factors (nutrient and water availability, density effects) may have affected the results of one or both of these studies which may have confounded the comparison.

These comparisons indicate that interspecific differences in morphological response, such as those between *T. repens* in the greenhouse studies and other stoloniferous species (SLADE & HUTCHINGS 1987b, LOVETT DOUST 1987), should be interpreted with care. Such differences may arise from the different resource trajectories applied in the studies of each of the species rather than from interspecific differences in morphological plasticity.

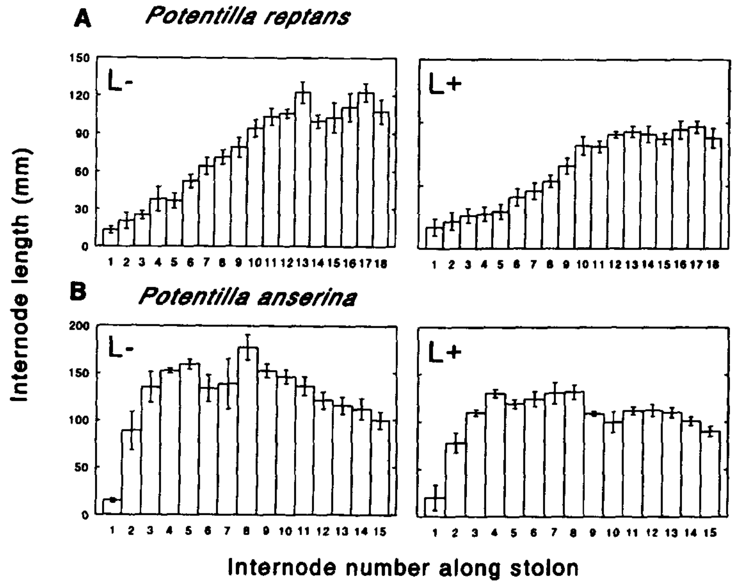

Fig. 3. Mean lengths of full-grown internodes (± s.e.) along primary stolons of (A) *Potentilla reptans* and (B) *P. anserina* under low (L-) and high (L+) levels of photosynthetic active radiation and red to far-red ratio. Results of a common garden study in which plants under high light were subjected to unshaded sunlight and plants under low light to 32% of full sunlight and a reduced red/far-red ratio of 0.25. From STUEFER (unpublished).

PLASTIC VERSUS NON-PLASTIC VARIATION

As noted above, morphological plasticity of a genotype is measured as the phenotypic response superimposed upon the variation which is not modified by the environmental conditions to which the plants are subjected. Here we present the results of two studies of stolon internode and rhizome lengths ("spacer" length) that show that the non-plastic variation in clonal plant morphology may be substantial. The origin of this variation is discussed.

The first example is from a study on morphological plasticity in two stoloniferous *Potentilla* species (J.F. STUEFER, unpublished). In a garden experiment, mother rosettes of *P. reptans* and *P. anserina* with one attached daughter stolon were subjected to full sunlight or to shading that reduced PAR to 32% and the red to far-red ratio to 0.25. In both species the stolon internode lengths were on average 20% longer in the shaded than in the full sunlight treatment (Fig. 3). The results also showed a systematic non-plastic variation in internode length along the stolon, exceeding the degree of plasticity by an order of magnitude or more (Fig. 3). In *P. reptans* the first internodes of a stolon successively increased in length until a maximum was reached after about ten internodes. In *P. anserina*, internodes exhibited some apparently random variation in length, but the most proximal and distal internodes tended to be relatively short.

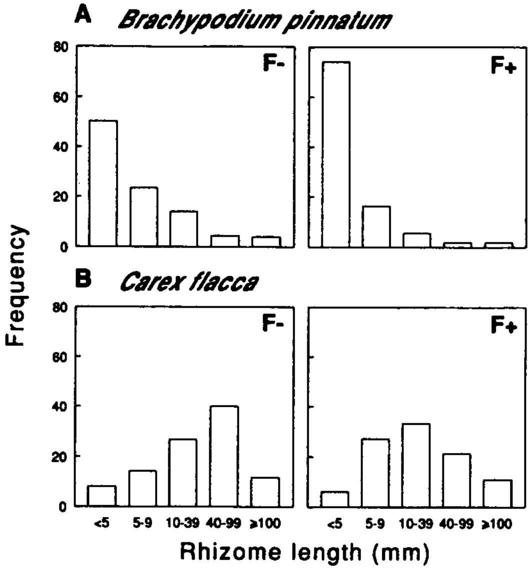

Fig. 4. Percentage frequency diagrams of rhizome lengths for (A) *Brachypodium pinnatum* and (B) *Carex flacca* under low (F-) and high (F+) levels of fertilization. Results of a greenhouse study in which the concentration of mineral nutrients supplied at high nutrition was ten times higher than at low nutrition. From DE KROON & KNOPS (1990).

In order to test whether differences in stolon internode length were statistically significant between treatments, STUEFER (unpubl.) applied a Repeated Measures Analysis of Variance model with internode position along the stolon as the repeated variable (see POTVIN et al. 1990, DONG 1993, DONG & DE KROON 1994). In this model the effects of within-stolon variation ("Within subject effect") are separated from plasticity ("Between subject effect") and the interaction between internode position and plasticity. STUEFER found that the plasticity in stolon internode length was highly significant for both species. However, from Fig. 3 it is immediately clear that only a minor part of the total variation in internode length can be explained by morphological responses due to treatment effects. Most of the variation in internode length seems to be the result of a species-specific pattern of stolon development. The non-plastic variation generated by this pattern is modified by environmental conditions only to a small extent.

A second example of non-plastic variation in clonal morphology is taken from the study by DE KROON & KNOPS (1990) on the morphological plasticity of two clonal graminoids from chalk grassland. In a greenhouse experiment, *Brachypodium pinnatum* and *Carex flacca* were subjected to two levels of nutrient availability. Both species exhibited a wide variation in the distribution of rhizome lengths (Fig. 4). The majority of the rhizomes of *B. pinnatum* were very short, resulting in the formation of clumps of shoots from which longer rhizomes occasionally grew out. On average, *C. flacca* formed longer rhizomes than *B. pinnatum* but with a wide variation around the mean. In both species there is a shift towards shorter rhizome lengths in response to higher levels of fertilization. However, while the changes in **mean** length were relatively large and significant, especially in *B. pinnatum*, the **variation** in length was only marginally changed (Fig. 4). Independent of treatment, every plant of *B. pinnatum* produced mostly short and only a few long rhizomes (DE KROON & KNOPS (1990). Thus, also in these rhizomatous species the level of non-plastic variation exceeded the level of morphological plasticity.

Fig. 5. The growth form of part of a *Carex bigelowii* rhizome system. Rhizomes may arise from buds at the ventral (lower) side of the shoot base, or at the dorsal (upper) side. The rhizomes of ventral (V) shoots are usually much longer than the rhizomes of dorsal (D) shoots. "Lateral" rhizomes (not drawn) are positioned at the left and right of the shoot base and are intermediate in length compared to ventral and dorsal rhizomes. From CARLSSON & CALLAGHAN (1990).

Non-plastic variation in rhizome length in graminoids appears to be related to the positioning of the buds at the base of the mother ramet below the soil surface. CARLSSON & CALLAGHAN (1990) found for *Carex bigelowii* that rhizomes arising from ventral buds, initiated at the lower (convex) side of the shoot base, are much longer than rhizomes arising from dorsal buds at the upper (concave) side (Fig. 5). This observation suggests that the orientation of the bud (upwards or downwards) may be an important determinant of the length of the rhizome to which the bud gives rise. This pattern may arise from the sensitivity of the rhizome apex to light: in some species the apex starts forming an aerial shoot in response to illumination (LEAKEY 1981) which terminates the elongation of the rhizome. Because the growth direction of dorsal buds is immediately upwards towards the soil surface, they inevitably give rise to short rhizomes. Ventral rhizomes can elongate further before their apex reaches the soil surface.

We experimentally tested the hypothesis that bud orientation in relation to the soil surface may explain a large part of the non-plastic variation in rhizome length in *Carex* species (DE KROON, DE BRUIN & DONG, unpubl.). Shoots of *C. flacca* and their subtending rhizome were fixed in sand either in their "normal" position, in which the ventral buds at the convex side of the shoot base were pointing downwards and dorsal buds at the concave side were pointing upwards, or in an "inverted" position in which the orientation of the ventral and dorsal buds was reversed. In addition, the shoots were planted at three different soil depths

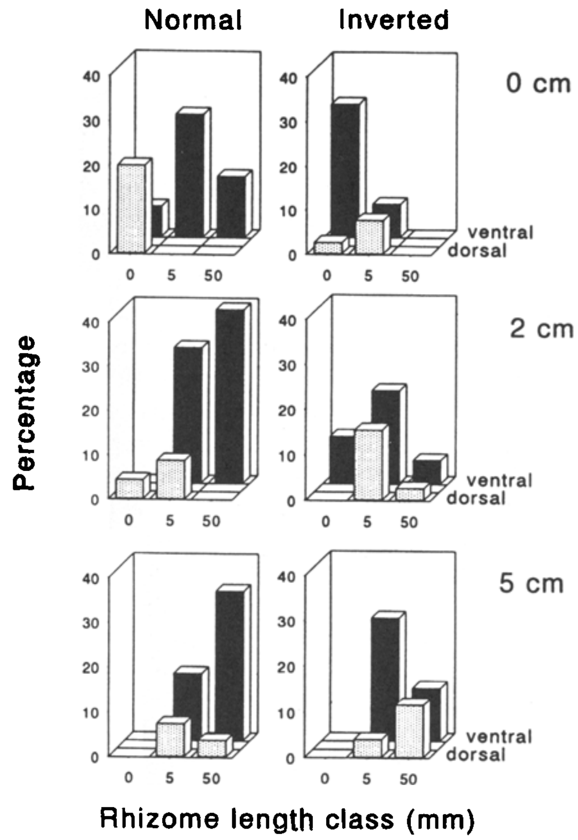

Fig. 6. The effects of shoot positioning ("normal" or "inverted") and the depth of the shoot base below the soil surface (0, 2 or 5 cm) on the lengths of the rhizomes that grow out from axillary buds at the shoot base in *Carex flacca*. In the "normal" position, ventral buds are pointing downwards and dorsal buds are pointing upwards; in the "inverted" position the orientation of the ventral and dorsal buds is reversed. The orientation of "lateral" buds, pointing to the left and right of the shoot base, is not changed by shoot positioning and their lengths are omitted from the figure. Percentage frequency distributions are given for rhizome lengths of three classes: < 5 mm (0), 5-49 mm (5) and ≥ 50 mm (50). From DE KROON, DE BRUIN & DONG (unpubl.).

to examine whether buds placed at a greater distance from the soil surface would produce longer rhizomes. At harvest, the lengths of all fully-grown rhizomes formed by the axillary buds at the shoot base were measured. In the "normal" position, ventral rhizomes were much longer than dorsal rhizomes (Fig. 6), similar to observations in *C. bigelowii* (CARLSSON & CALLAGHAN 1990). This difference between bud types emerged at all soil depths, though at greater depth overall rhizome length increased and rhizomes of the smallest length class were not produced. When the shoot was placed in an "inverted" position, the ventral buds gave rise to the shorter and the dorsal buds to the longer rhizomes, which is exactly the reverse compared to the normal position (Fig. 6). Thus a major part of the differences in length between the ventral and dorsal rhizomes can be explained by differences in the orientation of the axillary buds from which they grow.

Phyllotaxis determines that leaves and their axillary buds are produced on different sides of the shoot base. A consequence of this endogenous developmental pattern in rhizomatous plants is that it creates substantial variation in rhizome length within a single individual plant. Most of this variation will be apparent irrespective of the environmental conditions that the plant experiences.

THE SIGNIFICANCE OF MORPHOLOGICAL PLASTICITY IN HETEROGENEOUS ENVIRONMENTS

Despite the wide attention that morphological plasticity in clonal plants has received in recent years, our current knowledge of the ecological and evolutionary significance of plasticity is still far from complete. Many studies examined one or two genotypes of a species only, which gives no estimate of the mean level of plasticity in a population. Alternatively, studies with unknown genetic material may underestimate plasticity. In addition, plasticity experiments are usually carried out under only two levels of resource availability which may also underestimate plasticity if the responses describe an optimum curve (Fig. 2). None of the two common choices with respect to the genetic identity of the material provides information about the degree to which genotypes differ in plasticity. Hence, we yet know very little whether a critical prerequisite for the evolution of morphological plasticity, i.e. a significant genetic differentiation in phenotypic response, is met in clonal plants.

Nevertheless, some trends are discernable in the literature (DE KROON & HUTCHINGS, in press). Under higher light levels, most stoloniferous species have been shown to shorten their stolon internodes and to branch more intensively. Moderate responses of the magnitude seen in *Potentilla* species (20% shortening; Fig. 3) seem typical, irrespective of the genetic identity of the plant material that is used (compare for example SLADE & HUTCHINGS 1987a,b and DONG 1993). Only few species are more plastic, such as the grass *Cynodon dactylon* with stolon internodes that may reduce in length by more than 50% and branching intensity that may increase three-fold at higher light levels (DONG & DE KROON 1994). By contrast, very few rhizomatous species exhibit significant plasticity in clonal morphology to either light or nutrient availability (DE KROON & HUTCHINGS in press). The responses of *Brachypodium pinnatum* (Fig. 4) belong to the most vigorous reported to date.

In this paper we have shown that stolon internode and rhizome ("spacer") lengths may be extremely variable, and that this variation is hardly changed by the environmental conditions to which the plants are subjected (Figs. 3 and 4). Even if morphological plasticity is underestimated in experiments with clonal plants, it is likely that the degree of plastic variation is much smaller than the degree of non-plastic variation in a number of species. Ramet distribution patterns will be strongly influenced by this prominent non-plastic variation in morphological characters, which may override the plastic modifications generated by local environmental conditions (DE KROON & KNOPS 1990, VAN DER HOEVEN et al. 1990, CAIN 1994). In such cases the ecological significance of plasticity in clonal morphology in terms of foraging for favourable micro-habitats must be questioned.

The suggestion that morphological responses in clonal plants may have minor ecological significance is surprising because simulation studies have clearly demonstrated the potential benefits of highly plastic growth forms in heterogeneous environments (SUTHERLAND & STILLMAN 1988, OBORNY 1994, SAKAI unpubl.). Moreover, some studies have demonstrated genetic differentiation in morphological plasticity, suggesting that the evolution of morphological plasticity is a feasible option at least in some species. This raises the question why the plasticity of characters such as stolon internode length is not much greater in many clonal species. It is to be expected that selection would favour highly plastic genotypes that would eventually come to dominate the population.

Three complementary reasons may be responsible for this apparent lack of selection for high plasticity in clonal morphology. First, species-specific developmental patterns may result in substantial non-plastic variation in morphological characters, as shown above, which may hamper selection for increased plasticity (cf. SACHS 1988). For example, in *Carex bigelowii*, the responses of rhizome length to nutrient availability are constrained by the orientation of the buds from which the rhizomes develop (Fig. 5). CARLSSON & CALLAGHAN (1990) showed that the long ventral rhizomes increased further in length in response to fertilization while the responses of the short dorsal rhizomes were insignificant. Dorsal buds have an upward orientation so that the rhizomes to which they give rise to reach the soil surface and form a shoot almost immediately after elongation has started, irrespective of environmental conditions. The number of dorsal shoots increased at higher nutrient availability and CARLSSON & CALLAGHAN (1990) suggested that this may help the plant to exploit nutrient-rich patches. In *C. bigelowii* plasticity in the orientation of the buds may thus be of greater significance for shoot placement than the rhizome lengths per se.

Second, selection for high plasticity in clonal morphology may not have occurred because the non-plastic variation itself may be of ecological and demographic importance. CARLSSON & CALLAGHAN (1990) found for *C. bigelowii* that ventral shoots were larger and produced more daughter rhizomes but flowered less frequently than dorsal shoots. The two shoot types contribute to population growth rate in different ways, ventral shoots mainly by new rhizome formation and dorsal shoots by flowering (CARLSSON & CALLAGHAN 1991). In Swedish tundra the ventral shoots were demographically much more important than the dorsal shoots, but this may change in years in which the opportunities for seedling establishment are good. In *Brachypodium pinnatum*, the prominent endogenous variation in rhizome length results in a characteristic clumped distribution of shoots in the field (VAN DER HOEVEN et al. 1990). The shorter rhizomes that produce these clumps have many axillary buds that remain dormant (DE KROON & KNOPS 1990). These buds are likely to give rise to the shoots of future generations and permit the consolidation of the clumps. Longer rhizomes provide clonal expansion and the rapid formation of relatively tall shoots on the longer rhizomes may facilitate the establishment of the clone in unoccupied territory. Similar differences in shoot characteristics have been demonstrated between intra- and extravaginal tillers in *Festuca rubra* (HERBEN et al. unpubl.).

Third, selection for high plasticity in clonal plant morphology may not occur because our concept of habitat heterogeneity may be in error. Possibly, patches may not be meaningfully characterized by overall levels of resource availability that express their favourability, but rather as favourable for one and unfavourable for another resource. For example, in relatively open habitats, patches may either be exposed (receiving high light) and dry, or shaded (for instance by shrubs) and more moist. In habitats in which there is such a negative covariance in the spatial distribution of different resources, foraging for "favourable" patches by a high plasticity in clonal morphology will not be a feasible option. Rather, a reciprocal exchange of resources between ramets placed in **each** of the different patches may markedly stimulate growth in **all** patches (ALPERT & MOONEY 1986, FRIEDMAN & ALPERT 1991, STUEFER et al.

1994). Such increased performance will be enhanced by a "division of labour" in which roots and shoots forage for the resource that is locally most abundant (BIRCH & HUTCHINGS 1994, STUEFER et al. 1994). Indeed, foraging by root and shoot branching of a single ramet may be a faster and more effective means to exploit patches of high resource supply than foraging by plasticity in clonal morphology (HUTCHINGS & DE KROON 1994). In heterogeneous environments, physiological integration and a division of labour may be of greater ecological significance to clonal plants than a responsive clonal morphology.

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