
Plasticity in Morphology and Biomass Allocation in Cynodon dactylon, a Grass Species Forming Stolons and Rhizomes
Author(s): Ming Dong and Hans de Kroon
Source: *Oikos*, Vol. 70, Fasc. 1 (May, 1994), pp. 99-106
Published by: Wiley on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3545704
Accessed: 06/08/2014 17:04

OIKOS 70: 99–106. Copenhagen 1994

Plasticity in morphology and biomass allocation in Cynodon dactylon, a grass species forming stolons and rhizomes

Ming Dong and Hans de Kroon

Dong, M. and de Kroon, H. 1994. Plasticity in morphology and biomass allocation in *Cynodon dactylon,* a grass species forming stolons and rhizomes. – Oikos 70: 99–106.

Stolons and rhizomes may be important for the placement of leaves and roots in new microhabitats (foraging), as well as for the storage of resources. In a species which forms both types of structures, such as *Cynodon dactylon*, both such functions could be combined in a single structure, or rhizomes and stolons could exert different functions. We examine these functions in *C. dactylon*, by investigating plasticity in morphology and biomass allocation in response to variation in light and nutrient availability.

Both stolon and rhizome branching intensities were reduced in response to lower light and lower nutrient levels. Stolons and their internodes elongated greatly under lower light levels, but slightly shorter under lower nutrient levels. The lengths of rhizomes and their internodes did not respond significantly to nutrient availability. Only at low light levels did the plant form orthotropic shoots. Rhizomes failed to develop, and biomass allocation to stolons was slightly lower under low compared to high light intensity.

The morphology of stolons was more responsive than the morphology of rhizomes to resource supply. Biomass allocation to stolons, however, was less variable than allocation to rhizomes in response to light and nutrient treatments. These results support the contention that stolons enable *C. dactylon* to forage for light while rhizomes serve as organs for storage of resources and meristems.

These results are interpreted in terms of the efficiency of exploitation of light patches within the habitat of *C. dactylon*, and the ability to survive after unpredictable disturbances.

M. Dong and H. de Kroon, Dept of Plant Ecology and Evolutionary Biology, Univ. of Utrecht, P.O. Box 800.84, NL-3508 TB Utrecht, The Netherlands.

Morphological plasticity may be of critical importance for resource acquisition by plants (Grime et al. 1986). For clonal plants, in which ramets or "feeding sites" are interconnected by "spacers" (Bell 1984) such as stolon or rhizome segments, the plastic modifications of spacer length and branching intensity are of ecological significance. They determine the positioning of feeding sites in a patchy environment. Some stoloniferous species such as *Glechoma hederacea* (Slade and Hutchings 1987a, b) and *Lamiastrum galeobdolon* (Dong 1993), and rhizomatous species such as *Hydrocotyle bonariensis* (Evans 1992) have been found to produce longer spacers and to reduce their branching intensity under lower levels of light and/or nutrient availability. It has been suggested that these responses enable plants to place ramets selectively in resource-rich patches within their environment (foraging, sensu Hutchings and Slade 1988, de Kroon and Schieving 1990), thus enhancing the efficiency with which patchily-distributed resources are exploited (Cook 1985, Hutchings 1988, Sutherland and Stillman 1988; but see Hutchings and de Kroon 1994).

In this paper we investigate morphological plasticity in *Cynodon dactylon*, a grass species forming above-ground stolons and below-ground rhizomes simultaneously (Har-

Accepted 19 October 1993

ISSN 0030-1299
Printed in Denmark – all rights reserved

lan et al. 1969, Rawal and Harlan 1971, Jones 1985, Hanna 1992). In discussions of morphological plasticity, stolons and rhizomes are usually considered as organs with similar responses and functions (Sutherland and Stillman 1988, de Kroon and Schieving 1990). In a species like *C. dactylon* which produces both types of structures, this may not be true. Here three alternative hypotheses were tested.

(1) If stolon and rhizome tips are able to sense the quality of their microenvironments (Lovell and Lovell 1985, Hutchings and Slade 1988, Dong 1993), a stolon would be more likely to sense above-ground resources and a rhizome more likely to sense below-ground resources. Foraging responses (as described above) will be enhanced by the ability to sense the local conditions. We thus may hypothesize that the morphological characteristics of stolons such as total length, internode length and branching will be more responsive to variation in light levels than to variation in nutrient levels, while rhizome morphology will be more responsive to nutrients than to light availability.

(2) Rhizomes and stolons are homologous organs and both are modified stems (Hutchings and Mogie 1990). They may thus share the same physiological control of morphological plasticity (Hutchings and Slade 1988, Hutchings and Mogie 1990). In particular, the rhizomes and stolons of a *Cynodon dactylon* plant are interconnected, anatomically similar (Stiff and Powell 1974, Rogers et al. 1976, Jones 1985) and physiologically well-integrated (Forde 1966). Consequently, we may hypothesize that stolons and rhizomes will show an integrated morphological response to differences in resource supply and thus that stolons and rhizomes will show similar morphological responses to variations in light and nutrient availability.

(3) In addition to providing the plant with the ability to place ramets in different patches of a heterogeneous habitat, spacers may also serve as storage organs for buds and carbohydrates. This is particularly true for the rhizomes of perennial herbs (Grime 1979, Fitter 1986, Eriksson and Jerling 1990, de Kroon and Knops 1990). In a species like *C. dactylon* which has two types of spacers we may hypothesize that these functions will be separated, with stolons serving primarily as spacing organs and rhizomes primarily as storage organs. It would thus be expected that the stolons would be more plastic in morphological characteristics than the rhizomes. Because production of storage organs such as rhizomes is likely to be reduced under resource shortage (de Kroon and Knops 1990, Evans 1991, 1992), we would also expect that biomass allocation to rhizomes will be more plastic than biomass allocation to stolons in response to variations in resource availability.

These three hypotheses were tested in a garden experiment in which *C. dactylon* plants were subjected to two levels of light intensity and two levels of nutrient availability in a two-way factorial design. High levels of morphological plasticity are considered as evidence that the rhizomes or stolons serve a foraging function. Highly plastic allocation to a structure is in accordance with the function as a storage organ. Morphological plasticity and allocation may be uncorrelated in clonal plants (de Kroon and Schieving 1991).

Materials and methods

The species

Cynodon dactylon (L.) Pers. is a clonal, perennial, C_4 grass from tropical and warm-temperate areas, where it usually inhabits open locations which are subjected to frequent disturbances such as grazing, fire, flooding and drought (Ellenberg 1979, Jones 1985, Skerman and Riveros 1990, Hanna 1992). In principle, a *C. dactylon* plant is composed of three types of modules (products of a single apical meristem; White 1979, Cook 1985), namely plagiotropic stolons and rhizomes and orthotropic shoots. Each of these module types may be terminated by an orthotropic inflorescence. Stolons and rhizomes differ in morphology: stolons are thin and green and have macroscopic green leaves, while rhizomes are white and thick and have scale leaves. Occasionally, stolon apices may start growing underground and become modified into rhizomes, and vice versa, which changes the morphology abruptly. Each macroscopically distinguishable "node" of stolons and rhizomes (these are also referred to as "compound nodes") usually consists of three actual metamers (sensu White 1979) with very short internodes (Rawal and Harlan 1971, Jones 1985). Each node thus has three leaves and three axillary buds. However, in the present experiment it was observed that only one of these axillary buds was activated if the stolon or rhizome was branching. The axillary bud on a stolon, a rhizome and a shoot may give rise to either a stolon, a rhizome or an orthotropic shoot. Stolon and rhizome nodes and the base of orthotropic shoots all frequently form adventitious roots.

Experimental design

Plant material from a single clone of *C. dactylon* was collected at Igueste de San Andres, Tenerife, Spain, and propagated for six months in the greenhouse. The experiment was carried out with small plants initially consisting of a single stolon node with three leaves and attached adventitious roots. The experiment was conducted at the Uithof Botanical Garden, Utrecht, the Netherlands, from 31 May to 20 September 1991. The plants were grown in plastic containers 44 cm in diameter and 50 cm high, filled with river sand. Four treatments were applied, differing in the availability of light and nutrients, consisting of high light, high nutrient conditions (L+N+), high light, low nutrients (L+N–), low light, high nutrients (L–N+) and low light, low nutrients (L–N–). The high light level (L+) was unshaded daylight; the low light level (L–) was

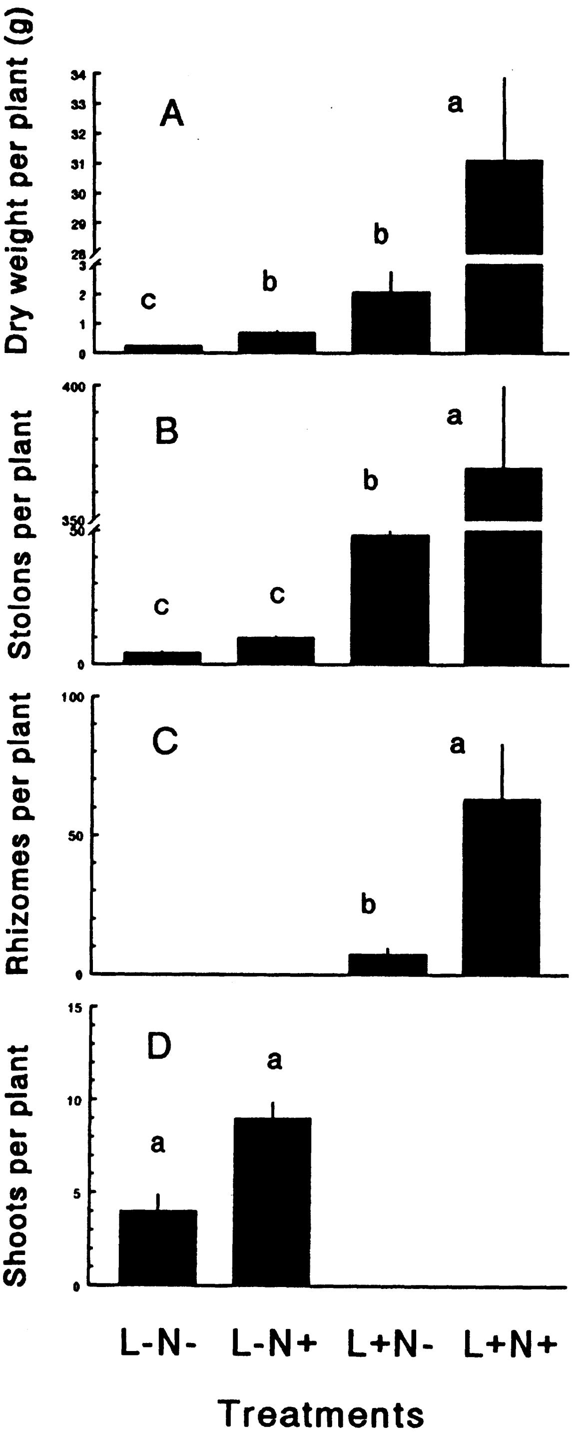

Fig. 1. (A) Dry weight (mean + SE), number (mean + SE) of (B) stolons, (C) rhizomes and (D) orthotropic shoots per plant grown at high (+) or low (–) light (L) and/or nutrient (N) levels. Bars sharing the same letter are not significantly different at p = 0.05 (Tukey grouping). Two-way ANOVA results for plant weight and the number of stolons are given in Table 1.

obtained using neutral shading cloth that transmitted ca 20% of daylight PAR. The high nutrient level (N+) was established by providing plants with a nutrient solution (4.37 g l^{-1} NH_4NO_3, 2.06 g l^{-1} $NaH_2PO_4.2H_20$ and 2.88 g l^{-1} KCl) (160 ml wk^{-1} $container^{-1}$) which was equivalent to 200 kg N, 60 kg P and 200 kg K ha^{-1} yr^{-1}. The low nutrient level (N–) was applied as a nutrient solution with the same volume but only 10% of the nutrient concentration of the high nutrient level. During the experiment the plants were watered as needed. Each treatment had eight replicates.

Harvesting and analyses

After nearly four months of growth the plants were harvested and the following characteristics were measured: the lengths of primary and secondary stolons and rhizomes, and their internodes. Number of stolons, rhizomes and orthotropic shoots were counted and the fate of the lateral meristems of primary stolons and rhizomes was determined. The dry weights of leaves, roots, stolons, rhizomes and stems of orthotropic shoots (excluding leaves and leaf sheaths) per plant were determined after drying at 75°C for a minimum of 48 h.

Analyses of percentage allocation have been criticised because they may obscure the relevant physiological causes behind differences in allocation patterns (cf. Tuomi et al. 1983), and allometric (size) effects on allocation (Samson and Werk 1986, Weiner 1988). A graphical size-regression approach or size-dependent allocation model has been suggested to avoid these problems (Samson and Werk 1986, Weiner 1988, Hartnett 1990) and to allow allocation to be validly related to morphological plasticity (de Kroon and Schieving 1991). Here we adopt this approach, and analyze stolon, rhizome and stem mass as functions of plant size. Plant size was expressed as the total weight of plant structures which are directly involved in resource acquisition, i.e. leaf and root. In an analysis of covariance (ANCOVA, procedure GLM, SAS 1985), a significant effect of treatment in addition to effect of size indicates that allocation differs significantly between treatments. When treatment effect was significant, relationships between weight of stolons, rhizomes and stems on the one hand and leaf + root mass on the other were examined by means of linear regression (REG procedure, SAS 1985). Allocation to certain plant structures is higher when the slope is steeper and/or the intercept is larger. For comparison, proportional allocation to plant structures was also investigated, using the ratio of the weight of these structures to the weight of leaves and roots (see Samson and Werk 1986, Hartnett 1990, de Kroon and Schieving 1991).

Branching intensities were calculated by dividing the number of secondary modules (stolons, rhizomes and shoots) formed by a single primary stolon or rhizome, by the number of nodes present on the primary stolon or rhizome. Other characteristics were analyzed by means of

Table 1. F-values of effects of light (L) and nutrients (N) on dry weight per plant (DWP), number of stolons per plant (NSP), stolon branching intensity (SBI), mean length of primary stolons (MLPS), mean length of secondary stolons (MLSS) and mean internode length of secondary stolons (MILSS). Numerator and denominator of degree of freedom (df) are given. Significance levels: *** = $p<0.001$, ** = $p<0.01$, * = $p<0.05$ and ns = $p>0.05$.

Effect	df	DWP	NSP	SBI	MLPS	MLSS	MILSS
L	1,28	38.6***	13.3***	31.1***	22.3**	103.6***	195.3***
N	1,28	34.6***	7.7**	4.9*	4.3*	9.9**	21.7***
L×N	1,28	32.4***	7.3**	2.7^{ns}	0.2^{ns}	1.1^{ns}	1.1^{ns}

one- or two-way ANOVA (GLM procedure, SAS 1985). Because internodes along stolons or rhizomes are not independent units, a Repeated Measures ANOVA using H-F-corrected P-values was employed to test for differences between internodes along primary stolons and primary rhizomes (SAS 1985, Potvin et al. 1990, Dong 1993).

Results

Overall plant performance

At the end of the experiment, plants growing under the most favourable condition (L+N+) formed up to seven generations of stolon modules, whereas plants under the least favourable condition (L–N–) formed only three. Plants growing under shade produced stolons with an upward curvature of their distal parts, and leaves that were twice as long as leaves formed under unshaded conditions. Plants flowered only under unshaded conditions. Dry weight per plant was markedly reduced under lower light intensity and/or lower nutrient availability (Fig. 1A; Table 1), and the low level of light reduced growth more strongly than the low level of nutrient availability.

The responses of the number of stolons to light and nutrients were similar to those of plant dry weight (Fig. 1B). However, the responses of the number of rhizomes and orthotropic shoots were different. Rhizomes were formed only under high light intensities, while shoots were formed only under low light intensities. The numbers of both rhizomes and shoots were reduced under lower nutrient availability, but only the response to nutrients of rhizomes was significant (Fig. 1C, D).

Branching intensities of stolons and rhizomes

There were significant effects of both light and nutrient availability on stolon branching intensity (Fig. 2A, Table 1). Under the most favourable conditions (L+N+), most of the axillary buds of primary stolons (90%) were activated, but under L–N– conditions the majority of the buds (70%) remained dormant. Under high light intensity nearly all of the activated stolon buds grew out to form lateral stolons and only a minor proportion gave rise to rhizomes. However, at low light level a significant proportion of the activated stolon buds grew out as orthotropic shoots.

Rhizome branching was significantly affected by nutrient availability (Fig. 2B). A considerable proportion of the rhizome buds remained dormant. Under high nutrient levels only about half of all the buds were activated, while this percentage was reduced to approximate 20% under low nutrient levels. Nearly all activated rhizome

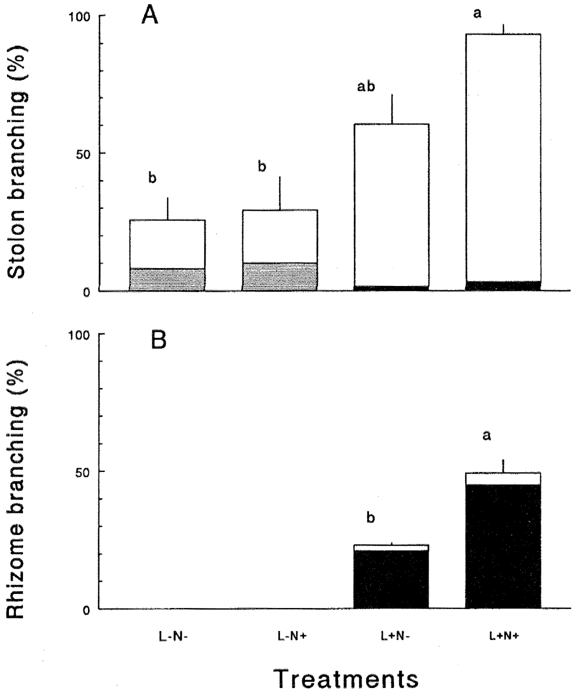

Fig. 2. Branching intensities (mean + SE) of (A) stolons and (B) rhizomes. Treatment codes as in Fig. 1. Bars sharing the same letter are not significantly different at p = 0.05 (Tukey grouping). Two-way ANOVA results for the stolon branching are given in Table 1. Open, solid and shaded parts of bars indicate buds which grew out as stolons, rhizomes and shoots, respectively.

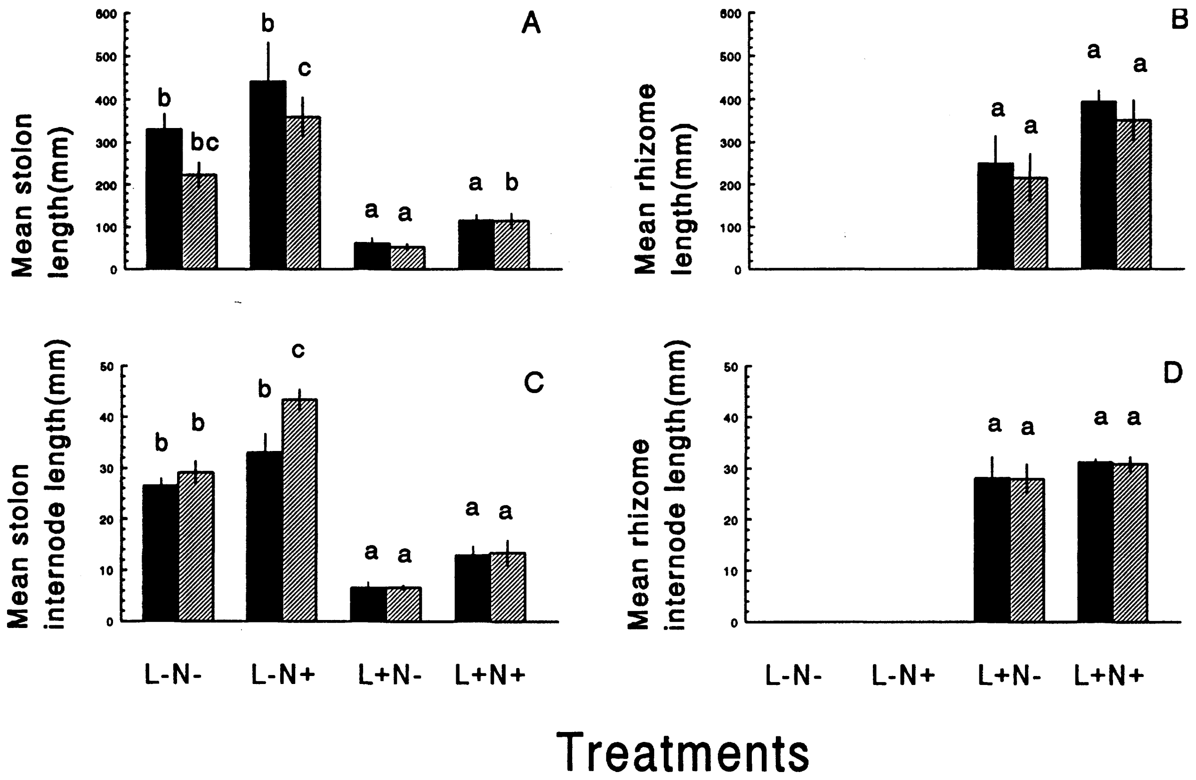

Fig. 3. Mean lengths (mean ± SE) and mean internode lengths (mean ± SE) of primary (solid bars) and secondary (hatched bars) stolons (A, C) and rhizomes (B, D). Treatment codes as in Fig. 1. For each characteristic, separately for primary and secondary structures, bars sharing the same letter are not significantly different at p = 0.05 (Tukey grouping). Full results of statistical tests are given in Tables 1 and 2.

buds formed lateral rhizomes, and only a small proportion grew out as stolons.

Table 2. Effects of light (L), nutrients (N) and position (P) on length of internodes along primary stolong (two-way) and rhizomes (one-way) analysed by means of Repeated Measures ANOVA (procedure GLM, Repeated Measures Option, SAS 1985, Potvin et al. 1990, Dong 1993). Numerator and denominator of degree of freedom (df) and the F-values are given. Significance levels: *** = $p<0.001$, ** = $p<0.01$, * = $p<0.05$ and ns = $p>0.05$. – = not applicable.

Effect	Primary stolon internode length		Primary rhizome internode length	
	df	F-value	df	F-value
Between subjects				
L	1,28	29.33***	–	–
N	1,28	7,25*	1,14	0.08^{ns}
L×N	1,28	1.89^{ns}	–	–
Within subjects				
P	5,140	30.25***	5,70	3.15*
P×L	5,140	3.98*	–	–
P×N	5,140	1.68^{ns}	5.70	3.23*
P×L×N	5,140	0.27^{ns}	–	–

Lengths of stolons, rhizomes and their internodes

Under low light levels primary and secondary stolons were considerably longer than under high light levels. By contrast, lower levels of nutrient availability slightly shortened the stolons (Fig. 3A, Table 1). The magnitude of the effect of light was larger than that of nutrients. In contrast to stolons, the lengths of primary and secondary rhizomes were not significantly affected by variation in nutrient availability at p = 0.05 (Fig. 3B). No data are available from this experiment on the effect of light availability on rhizome lengths.

The differences in stolon length between treatments were largely due to the responses in stolon internode length. Internode lengths of primary and secondary stolons were longer under low compared to high light levels, while low nutrient availability shortened the stolon internodes (Fig. 3C, Tables 1, 2). In contrast to stolons, internode lengths of primary and secondary rhizomes were unaffected by nutrient availability (Fig. 3D, Table 2). Internode lengths showed a significant effect of position along the primary stolons and rhizomes which significantly depended on light and nutrient treatments, respectively (Table 2).

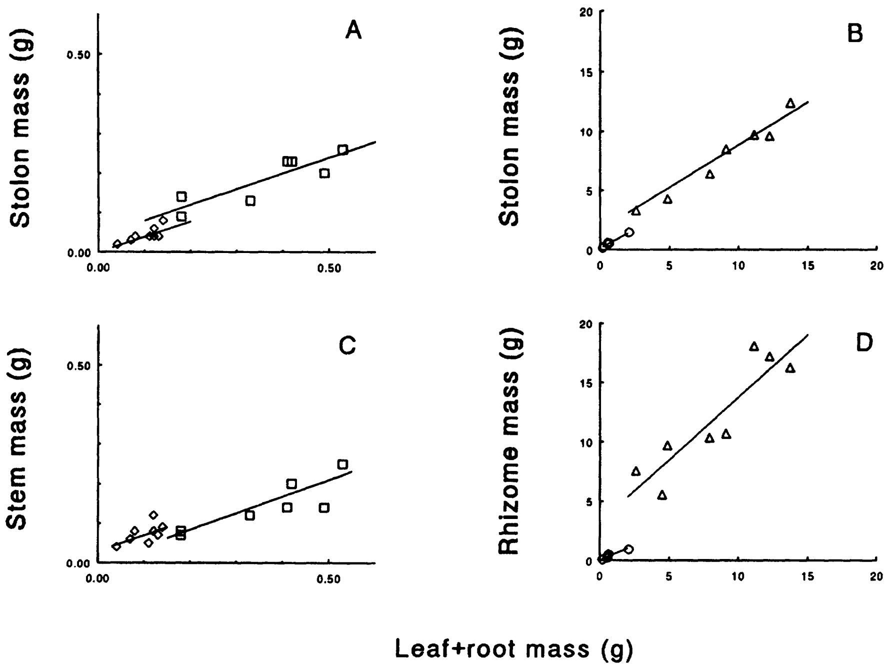

Fig. 4. Stolon mass (A, B), stem mass (C) and rhizome mass (D) as a function of leaf + root mass. The ratio of the scales of y- to x-axes is the same for all four panels. See Table 3 for the results of the statistical test. The symbols ◇, □, ○ and △ depict the treatments L–N–, L–N+, L+N– and L+N+, respectively.

Table 3. (A) Linear regression analyses between stolon mass (M_{sto}), rhizome mass (M_{rhi}) and stem mass (M_{ste}) and leaf + root mass (M_{l+r}) in *C. dactylon*. Regression lines are given in Fig. 4. (B) Proportional allocation to stolons (PA_{sto}), rhizomes (PA_{rhi}) and to stems (PA_{ste}). The proportional allocation to plant structures is the ratio of the weight of these structures to the weight of leaves + roots. Treatment codes as in Fig. 1. For each row, the data sharing the same lower-case letter are not significantly different at p = 0.05. For each column, the slopes sharing the same capital letter are not significantly different at p = 0.05. None of the intercepts was significantly different from zero. – = not applicable.

	L+N+	L+N–	L–N+	L–N–
(A) Regression parameters				
$M_{sto} = m\ M_{l+r} + b$				
Slope (m)	0.72^{aA}	0.64^{aA}	0.40^{bA}	0.39^{bA}
Intercept (b)	1.69	0.11	0.04	0.00
$M_{rhi} = m\ M_{l+r} + b$				
Slope(m)	1.05^{aB}	0.484^{bB}	–	–
Intercept (b)	3.28	0.06	–	–
$M_{ste} = m\ M_{l+r} + b$				
Slope (m)	–	–	0.42^{aA}	0.40^{bA}
Intercept (b)	–	–	0.00	0.03
(B) Proportional allocation				
PA_{sto}	$0.99(0.09)^{a}$	$0.85(0.05)^{a}$	$0.53(0.05)^{b}$	$0.45(0.04)^{b}$
PA_{rhi}	$1.61(0.21)^{a}$	$0.29(0.12)^{b}$	–	–
PA_{ste}	–	–	$0.4\ (0.03)^{a}$	$0.77(0.08)^{b}$

Biomass allocation to stolons, rhizomes and stems

There was usually a strong positive correlation between the biomasses of stolons, rhizomes and stems and the biomass of leaves and roots (Fig. 4A-D, Table 3). ANCOVA results showed that effect of light treatment on allocation to stolon and effect of nutrient treatments on allocation to rhizomes and stems were significant in addition to effects of size. None of the regression lines had intercepts that were significantly different from zero at p = 0.05. The slopes of the regression lines were lower under lower resource levels, indicating that allocations to stolons, rhizomes and stems were reduced as resources were in short supply. This reduction was significantly larger for rhizomes than for stolons.

Changes in proportional allocation between treatments (Table 3) accorded with those of the size-dependent allocation patterns (Fig. 4A-D).

Discussion

We have shown that the stolon morphology of *C. dactylon* was highly plastic in response to light availability. This accords with the 'foraging' responses observed for some other species (Slade and Hutchings 1987b, Dong 1993, Hutchings and de Kroon 1994). The morphology of the rhizomes, and especially rhizome lengths, showed little plasticity in response to resource supply, but biomass allocation to rhizomes was reduced more strongly under short resource supply than biomass allocation to stolons. These results are in accordance with the third hypothesis that stolons serve as foraging organs and that rhizomes have predominantly a storage function. The implications of these results are discussed below.

Responses of stolons and shoots

C. dactylon stolons and their internodes were two to three times longer under low than under high light intensity. The magnitude of this shade-induced elongation is much greater than what has been found for other stoloniferous herbs (e.g. *Glechoma hederacea*, Slade and Hutchings 1987b; *Lamiastrum galeobdolon*, Mitchell and Woodward 1988, Dong 1993). Moreover, *C. dactylon* plants showed shade-induced orthotropic shoot production, leaf elongation and upward distal curvature of stolons. These responses may be of ecological importance because in the field they may provide the plant with the ability to position its leaves further in the high light zone in the top of the canopy. Data taken from literature on clonal plants show that spacers generally elongate by no more than 50% in response to shading, and these relatively small responses have been considered to be inadequate for placing ramets in high-light patches in a selective way (Hutchings and de Kroon 1994). The much larger elongation responses observed in this experiment on *C. dactylon*, together with the formation of orthotropic shoots and lower branching under shade, is likely to result in a much more effective exploitation of high light patches by *C. dactylon*, compared to other clonal herbaceous species. These responses may be particularly beneficial in the dynamic, patchy environments in which *C. dactylon* is usually found.

In contrast to the responses to light intensity, the stolons and their internodes were longer under high compared to low nutrient availability. This elongation may be interpreted as a simple growth response (see Hutchings and de Kroon 1994): a larger structure is formed when more resources are available to the plant. Stolons of *C. dactylon* are unable to forage selectively for nutrient-rich patches within the habitat.

Responses of rhizomes

The lengths of *C. dactylon* rhizomes and their internodes did not show significant responses to variation in nutrient availability. Because the plant failed to develop rhizomes under shaded conditions, it is not possible in the present experiment to investigate morphological responses of the rhizomes to shading. However, the results from a subsequent study with *C. dactylon* indicated that the lengths of its rhizomes and their internodes do not respond significantly to shading either (Dong et al. unpubl.). The lack of responses of rhizome length of *C. dactylon* indicates that rhizomes are unable to place ramets of this species selectively within the habitat.

Rhizomes of plants, especially of perennial herbs, are usually thought to store buds and resources in order to be able to regenerate after habitat disturbances (Grime 1979). Our results are in agreement with this notion. In spite of the lack of morphological plasticity, biomass allocation to rhizomes was strongly reduced under low nutrient availability, while the small plants under low light intensities did not form any rhizomes at all. Allocation to rhizomes also showed a strong size-dependent effect, especially under L+N+ conditions. Such a strong reduction in rhizome size with decreasing plant size and resource availability may be expected for storage organs that are more expensive to produce than stolons and shoots (Fitter 1986, Chapin et al. 1990). Moreover, the rhizomes maintained a large percentage of their buds in a state of dormancy, even under the most favourable conditions, giving the plants the potential to regenerate after habitat disturbance. Only when plants are very small and/or grow under low resource levels, is this storage function compromised.

Different functions of rhizomes and stolons

The different responses shown by the rhizomes and stolons of *C. dactylon* plants suggest that they have different functions, foraging for light in the case of stolons and storing meristems and carbohydrates in the case of rhizomes. Such differentiation of two closely related homologous organs has not been demonstrated before.

This separation of functions between rhizomes and stolons may be strategically beneficial in the grassland habitats occupied by *C. dactylon*, which are characterized by high light intensities at the soil level due to frequent disturbances. In shaded patches of habitat, the plant may effectively forage for light by plastic changes in stolon morphology and also by shifting biomass allocation from rhizomes to orthotropic shoots. In addition to intensive exploitation of light patches by means of plastic stolon morphology, the plant forms rhizomes which may help to survive unpredictable disturbances.

Acknowledgements – We thank H. J. During and M. J. A. Werger for valuable suggestions in the course of the experiment and critical comments on the manuscript, and L. Brandi and M. G. Pierdominici for assistance during measurements. HdK acknowledges financial support from the Royal Netherlands Academy of Sciences.

References

Bell, A. D. 1984. Dynamic morphology: a contribution to plant population ecology, – In: Dirzo, R. and Sarukhan, J. (eds), Perspectives on plant population ecology. Sinauer, Sunderland, MA, pp. 48–65.

Chapin, F. S. III, Schulze, E.-D. and Mooney, H. A. 1990. The ecology and economics of storage in plants. – Annu. Rev. Ecol. Syst. 21: 423–47.

Cook, RE. 1985. Growth and development in clonal plant population. – In: Jackson, J. B. C., Buss, L. W. and Cook, R. E. (eds), Population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT, pp. 259–296.

de Kroon, H. and Knops, J. 1990. Habitat exploration through morphological plasticity in two chalk grassland perennials. – Oikos 59: 39–49.

– and Schieving, F. 1990. Resource partitioning in relation to clonal growth strategy. – In: van Groenendael, J. and de Kroon, H. (eds), Clonal growth in plants: Regulation and function. SPB Acad. Publishing, The Hague, pp. 113–130.

– and Schieving, F. 1991. Resource allocation patterns as a function of clonal morphology: a general model applied to foraging clonal plant. – J. Ecol. 79: 519–530.

Dong, M. 1993. Morphological plasticity of the clonal herb *Lamiastrum galeobdolon* (L.) Ehrend & Polatschek in response to partial shading. – New Phytol. 124: 291–300.

Ellenberg, H. E. 1979. Zeigerwerte der Gefässpflanzen Mitteleuropas. – Scripta Geobot. 9.

Eriksson, O. and Jerling, L. 1990. Hierarchical selection and risk spreading in clonal plants. – In: van Groenendael, J. and de Kroon, H. (eds), Clonal growth in plants: Regulation and function. SPB Academic Publ., The Hague, pp. 79–94.

Evans, J. P. 1991. The effect of resource integration on fitness related traits in a clonal dune perennial, *Hydrocotyle bonariensis*. – Oecologia 86: 286–275.

– 1992. The effect of local resource availability and clonal integration on ramet functional morphology in *Hydrocotyle bonariensis*. – Oecologia 89: 265–276.

Fitter, A. H. 1986. Acquisition and utilization of resources. – In: Crawley, M. J. (ed.), Plant ecology. Blackwell, Oxford, pp. 376–406.

Forde, B. J. 1966. Translocation in grass – I. Bermudagrass. – N. Z. J. Bot. 4: 479–495.

Grime, J. P. 1979. Plant strategies and vegetation processes. – Wiley, Chichester.

– , Crick, J. C. and Rincon, J. E. 1986. The ecological significance of plasticity. – In: Jennings, D. H. and Trewavas, A. J. (eds), Plasticity in plants. Biologists Limited, Cambridge, pp. 5–29.

Hanna, W. W. 1992. *Cynodon dactylon*. – In: 't Mannetje, L. and Jones, R. M. (eds), Plant resources of south-east Asia. No 4: Forages. Pudoc, Wageningen, pp. 100–102.

Harlan, J. R., de Wet, J. M. J. and Richardson, W. L. 1969. Hybridization studies of *Cynodon* from east Africa and Malagasy. – Am. J. Bot. 56: 944–950.

Hartnett, D. C. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. – Oecologia 84: 254–259.

Hutchings, M. J. 1988. Differential foraging for resources and structural plasticity in plant. – Trends Ecol. Evol. 3: 200–204.

– and Slade, A. J. 1988. Morphological plasticity, foraging and integration in clonal perennial herbs. – In: Davy, A. J., Hutchings, M. J. and Watkinson, A. R. (eds), Plant population ecology. Blackwell, Oxford, pp. 83–109.

– and Mogie, M. 1990. The spatial structure of clonal plants: control and consequences. – In: van Groenendael, J. and de Kroon, H. (eds), Clonal growth in plants: Regulation and function. SPB Academic Publ., The Hague, pp. 57–76.

– and de Kroon, H. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. – Adv. Ecol. Res. 25.

Jones, C. A. 1985. C_4 grasses and cereals: growth, development, and stress response. – Wiley, New York.

Lovell, P. H. and Lovell, P. J. 1985. The importance of plant form as a determining factor in competition and habitat exploitation. – In: White, J. (ed.), Studies in plant demography, A festschrift for John L. Harper. Academic Press, New York, pp. 209–221.

Mitchell, P. L. and Woodward, F. I. 1988. Responses of three woodland herbs to reduced photosynthetically active radiation and low red to far-red ratio in shade. – J. Ecol. 76: 807–825.

Potvin, C., Lechowicz, M. J. and Tardif, S. 1990. The statistic analysis of ecophysiological response curves obtained from experiments involving repeated measure. – Ecology 71: 1389–1400.

Rawal, K. M. and Harlan, J. R. 1971. The evolution of growth habit in *Cynodon* L. C. Rich (Gramineae). – Ill. State Acad. Sci. 64: 110–118.

Rogers, R. A, Dunn, J. H. and Brown, M. F. 1976. Ultrastructural characterization of storage organs of zoysia and bermudagrass. – Crop Sci. 16: 639–642.

Samson, D. A. and Werk, K. S. 1986. Size-dependent effects in the analysis of reproductive effort in plants. – Am. Nat. 127: 667–680.

SAS 1985. SAS/STAT guide for personal computers version 6 Edition. – SAS Inst. Inc., Cary, NC.

Skerman, P. J. and Riveros, F. 1990. Tropical grasses. – Rome.

Slade, A. J. and Hutchings, M. J. 1987a. The effect of nutrient availability on foraging in the clonal herb *Glechoma hederacea*. – J. Ecol. 75: 95–112.

– and Hutchings, M. J. 1987b. The effect of light intensity on foraging in the clonal herb *Glechoma hederacea*. – J. Ecol. 75: 639–650.

Stiff, M. L. and Powell, J. B. 1974. Stem anatomy of turfgrass. – Crop Sci. 14: 181–6.

Sutherland, W. J. and Stillman, R. A. 1988. The foraging tactics of plants. – Oikos 52: 239–244.

Tuomi, J., Harala, T. and Haukioja, E. 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. – Am. Zool. 23: 25–34.

Weiner, J. 1988. The influence of competition on plant reproduction. – In: Lovett Doust, J. and Lovett Doust, L. (eds), Plant reproductive ecology – pattern and strategies. Oxford Univ. Press, Oxford, pp. 228–245.

White, J. 1979. The plant as a metapopulation. – Annu. Rev. Ecol. Syst. 10: 109–45.