



The role of plasticity in resource capture by plants

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Abstract. Comparative experiments measuring the form and extent of plant responses to environmental factors allow an ecologically important distinction to be made between morphological plasticity and cellular acclimation. The two phenomena are associated with different sets of plant traits with which they occur with highest fidelity and potency at opposite ends of productivity gradients. A trade-off between scale and precision occurs with respect to the responses of plants to patchiness in resource supply and this provides valuable predictors of the status achieved by species in plant communities.

Key words: cellular acclimation, defoliation, morphological plasticity, phylogeny, plant community structure, resource foraging, screening tests, sets of traits, tradeoffs

Consequences of developmental plasticity for higher organizational levels

For both animals and plants there is abundant evidence of major developmental changes in the structure and functional characteristics of individuals as a consequence of exposure to particular environmental factors. The potential for change in the expression of the phenotype is also evident in the differences that can be observed between juvenile and mature individuals of identical genotype. In view of this evidence of the profound changes that can arise from plasticity it is interesting to consider why so often it is genetic variation within and between populations and speciation, rather than the phenotypic plasticity of individuals, that occurs as the dominant evolutionary response to environmental variation. The most likely explanation for this phenomenon is that there are limits to what organisms can achieve through plastic response. The purpose of this paper is to explore the nature of the constraints that determine not only the limits within which plasticity can contribute to the fitness of individuals but also the form in which plasticity can be expressed. In order to

restrict this agenda to manageable proportions attention will be restricted to the role of plasticity in the capture of resources by the root and shoot systems of plants.

Theory

One publication (Bradshaw, 1965) deserves special attention in any attempt to trace the development of our current understanding of plasticity in plants. Bradshaw recognised two forms of plasticity – morphological and physiological – with different mechanisms, resource costs and ecological implications. The first is essentially meristematic in character and involves replacement of existing tissues by new plant parts with different characteristics: it appears to represent a high-cost solution to a change in environment. The second – physiological plasticity – occurs in differentiated tissues and is imperceptible by eye. It is usually associated with a change in properties brought about by reversible subcellular rearrangements: here the costs are lower and the response can be much more rapidly achieved than in morphological plasticity although, because change occurs in existing cells there is little opportunity for this form of plasticity to result in the spatial adjustments that are often a key component of successful plant reactions to certain types of environmental variation.

Plasticity mechanisms are unlikely to evolve independently of habitat and they cannot be viewed in isolation from the selection mechanisms that operate in parallel on other plant traits. This has led to the hypothesis (Grime, 1977; Grime *et al.*, 1986) that the two forms of plasticity recognised by Bradshaw have consistent associations with distinct sets of traits that coincide with particular habitats and ecologies. The most important feature of this hypothesis is the prediction that morphological plasticity will be pre-eminent in plants of resource-rich productive habitats where the activities of the plants themselves generate a very dynamic spatial mosaic of resources above and below ground and there is continuous replacement of those leaves and roots that have become trapped in the depleted zones. Such high-cost foraging is unlikely to be sustainable in slow-growing plants of unproductive habitats and here we can predict that cellular acclimation will be an important part of the homeostatic mechanisms maintaining tissue viability and function in long-lived cells. This simple dichotomy has major significance for the recognition of primary functional types in plants and in Table 1 the benefits and ecological costs of the morphologically plastic responses to resource stress of competitors and ruderals (*sensu* Grime, 1977) are compared to those predicted for the stress-tolerators which are expected to rely on acclimation.

Table 1. Morphogenetic responses to desiccation, shading or mineral nutrient stress of competitive, stress-tolerant and ruderal plants and their ecological consequences in three types of habitat

Strategy	Response to stress	Consequences		
		Habitat 1 ^a	Habitat 2 ^b	Habitat 3 ^c
Competitive	Large and rapid changes in root:shoot ratio, leaf area and root surface area	Tendency to sustain high rates of uptake of water and mineral nutrients to maintain dry matter production under stress and to succeed in competition	Tendency to exhaust reserves of water and/or mineral nutrients both in the rhizosphere and within the plant: etiolation in response to shade increases susceptibility to fungal attack	Failure rapidly to produce seeds reduces chance of rehabilitation after disturbance
Stress-tolerant	Changes in morphology slow and often small in magnitude	Overgrown by Competitors	Conservative utilisation of water, mineral nutrients and photosynthate allows survival over long periods in which little dry matter production is possible	
Ruderal	Rapid curtailment of vegetative growth and diversion of resources into seed production		Chronically low seed production fails to compensate for high rate of mortality	

^a In the early successional stages of productive, undisturbed habitats (stresses mainly plant-induced and coinciding with competition).

^b In either continuously unproductive habitats (stresses more or less constant and due to unfavourable climate and/or soil) or the late stages of succession in productive habitats.

^c In severely disturbed, potentially productive habitats (stresses either a prelude to disturbance, e.g. moisture stress preceding drought fatalities or plant-induced between periods of disturbance).

An experimental test

From the foregoing theoretical ideas it is clear that one way to test the functional significance of plasticity is to measure the fidelity with which morphological plasticity and cellular acclimation are each associated with a different

and predictable set of plant traits. One such test is available from a screening experiment conducted on 53 vegetative traits in 43 common British plants of contrasted ecology (Grime *et al.*, 1997). This programme included measurements of the scale and precision with which the leaf canopy and the root system of isolated plants responded to the introduction of standardised patchiness in, respectively, light intensity (and quality) and mineral nutrient concentration. The main feature of the results of these tests was the emergence in a PCA of a first axis accounting for 22% of the variation in all traits and associating variation in the magnitude of root and shoot morphological plasticity with a syndrome incorporating plant growth rate, leaf life-span, leaf chemistry, resistance to herbivory and decomposition rate. In this dataset, the extent of morphological plasticity in the leaves and root system was found to achieve higher values at the upper extremity of a productivity axis which entrains other fundamental plant attributes, several of which have obvious relationships not only to plant fitness but also to aspects of the functioning of ecosystems such as carbon storage, nutrient cycling and resistance and resilience following herbivore attack or exposure to extreme events. The screening programme did not include measurements of cellular acclimation but there is an extensive literature associating this form of plasticity with the tissues of slow-growing plants of unproductive habitats (e.g. Levitt, 1956; Mooney and West, 1964; Strain and Chase, 1966; Larsen and Kershaw, 1975).

On this basis and in the light of other comparative studies (e.g. Lambers and Poorter, 1992; Reich *et al.*, 1992) we can form the tentative conclusion that morphological plasticity and cellular acclimation reach full expression at opposite ends of a spectrum of plant functional types which in terms of resource processing range from 'the acquisitive' to 'the retentive' and correspond respectively to highly productive and chronically unproductive vegetation.

Plasticity, foraging, and plant community structure

As we have seen in the preceding section, comparative studies of the responses of plants of contrasted ecology are informative about the way that the expression of plasticity changes with habitat productivity. Similar methods can be used to assess how plasticity is related to the dominance hierarchies in plant communities. Figure 1 presents data from an experiment in which the magnitude of root and shoot foraging in eight herbaceous species was measured in a standardised patchy environment, and the results were compared with the status each attained when the same eight species were grown together on fertile soil in an equiproportional mixture for 16 weeks. The results show that the status of a species in a productive perennial community is predictable from the foraging behavior of its roots and the shoots. As we might expect, the covariance between

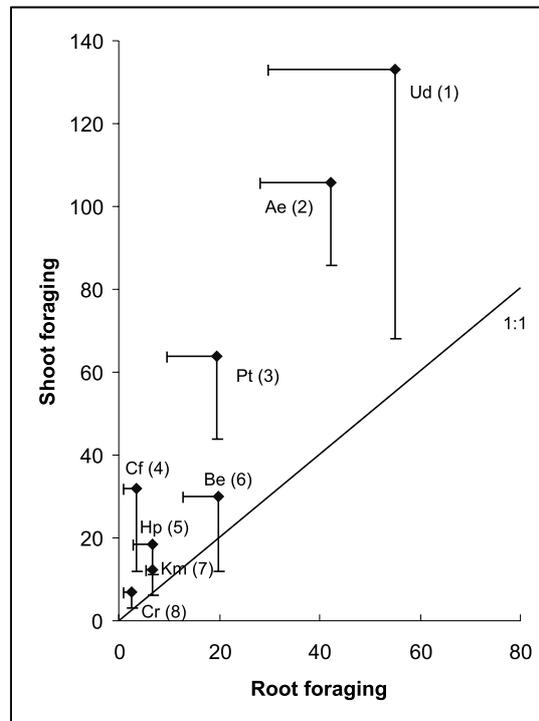


Figure 1. The relationship between root and shoot responses to resource heterogeneity in eight herbaceous species. A description of the methods used to expose the plants to resource patchiness is provided in Campbell, *et al.* (1991). Scales of foraging by the roots and shoots in the foraging assays are expressed as the respective increments in biomass (mg) to two undepleted quadrants, which in both assays constitute 50% of the available volume. The numbers in brackets refer to the species ranking in a conventional competition experiment in which all eight species were grown together in an equiproportional mixture on fertile soil for 16 weeks. The vertical and horizontal lines are 95% confidence limits. The species are: Ae, *Arrhenatherum elatius*; Be, *Bromopsis erecta*; Cf, *Cerastium fontanum*; Cr, *Campanula rotundifolia*; Hp, *Hypericum perforatum*; Km, *Koeleria macanthra*; Pt, *Poa trivialis*; Ud, *Urtica dioica*.

root and shoot foraging displays a consistent tendency for the scale of leaf canopy adjustment to exceed that of the root system. This, of course, arises from the freedom of movement of leaves in air and the encasement of roots in soil.

So far in examining the results of the screening of root and shoot responses to resource patchiness it has been convenient to focus on the ability of the plant to direct growth into the undepleted sectors of the environment and to express the results simply in terms of the total increment of tissue to the rich patches. As we have seen this confirms the prediction that success in dominating a productive plant community is associated with the potential to locate large masses of foliage and roots in resource-rich patches above and below ground. We might also expect that dominance will arise from the *precision* with which shoots and roots

discriminate between rich and poor patches. However this hypothesis is immediately falsified by re-examination of the data in the experiment comparing the eight species. Precision, expressed as the *proportion* of the new tissue which becomes located in the rich patches is higher in the species that occupy a subordinate position in the dominance hierarchy. This has led to the conclusion (Campbell *et al.*, 1991) that there is a trade-off between scale and precision in resource foraging and that there is genetic predisposition of dominant and subordinate roles in communities. According to this interpretation, fitness in potential dominants involves the construction of arterial root and shoot structures that are relatively insensitive to fine-grained patchiness in resources but are an essential prerequisite for monopoly of resource capture from a large volume of habitat. In contrast, subordinates appear to have a greater potential for precise, fine-grained foraging which may allow widespread coexistence with dominants but commits them to a minor status in the vegetation and can lead to their local extinction where the vigour of the dominants is unconstrained.

Plasticity, foraging and phylogeny

Foraging for light

In Figure 2 precision of shoot response to patchiness in light is compared in 43 species and a comparison is drawn between monocotyledons and dicotyledons. Differences are evident in both groups but the majority of the broad-leaved plants achieve greater precision than the grasses. This pattern coincides closely with differences in the position of the shoot meristems. Where the growing points are carried aloft as in *Galium aparine*, continuous monitoring of the light environment occurs at positions within the canopy close to where new leaves arise: this satisfies the conditions necessary for precise foraging for light. Employing the same criteria, it is not surprising that the majority of turf grasses exhibit low foraging precision; the basal meristems of these grasses are too remote from the leaves they subtend to allow fine adjustments in position. Such inflexibility is not exclusive to the monocotyledons however; a similar constraint clearly operates in rosette forbs such as *Pilosella officinalis* and *Plantago lanceolata* where each successive leaf originates from near the ground surface.

It is not difficult to identify the past and continuing selection forces responsible for the imprecise foraging by the shoots of many monocotyledons. Especially in the turf-grasses, the basal positions of the meristems severely limit the directional control of leaf foraging for light but they confer a strong selective advantage in pastures by providing the basis for rapid recovery following grazing by vertebrates. Within both the monocotyledons and dicotyledons we have examined, there is evidence of a trade-off between precision

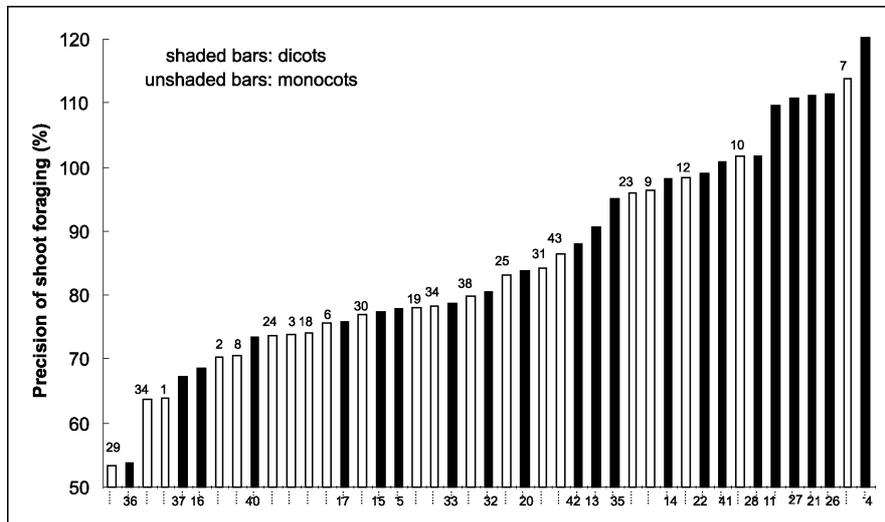


Figure 2. Comparison of 43 species with respect to the precision of leaf canopy adjustment to the imposition of a patchy light environment. A description of methods is provided in 268. Precision is expressed as the increment to shoot biomass in unshaded quadrants as a percentage of total shoot increment. Note that values can exceed 100% because of the capacity of some of the shoots formed prior to the introduction of shading to move phototropically. (1) *Agrostis capillaris*; (2) *Anisantha sterilis*; (3) *Anthoxanthum odoratum*; (4) *Anthriscus sylvestris*; (5) *Arabidopsis thaliana*; (6) *Arrhenatherum elatius*; (7) *Brachypodium pinnatum*; (8) *Briza media*; (9) *Bromopsis erecta*; (10) *Carex flacca*; (11) *Campanula rotundifolia*; (12) *Catapodium rigidum*; (13) *Centaurea scabiosa*; (14) *Cerastium fontanum*; (15) *Chamerion angustifolium*; (16) *Chenopodium album*; (17) *Conyza canadensis*; (18) *Dactylis glomerata*; (19) *Deschampsia flexuosa*; (20) *Digitalis purpurea*; (21) *Dryas octopetala*; (22) *Epilobium hirsutum*; (23) *Eriophorum vaginatum*; (24) *Festuca ovina*; (25) *Festuca rubra*; (26) *Galium aparine*; (27) *Helianthemum nummularium*; (28) *Helianthus annuus*; (29) *Helictotrichon pratense*; (30) *Holcus lanatus*; (31) *Koeleria macrantha*; (32) *Leontodon hispidus*; (33) *Lotus corniculatus*; (34) *Lolium perenne*; (35) *Origanum vulgare*; (36) *Pilosella officinarum*; (37) *Plantago lanceolata*; (38) *Poa annua*; (39) *Poa trivialis*; (40) *Rumex acetosella*; (41) *Thymus polytrichus*; (42) *Urtica dioica*; (43) *Zea mays*.

of foraging for light and the capacity to recover from defoliation. It is important to recognise however, that this trade-off is not manifested as a universal divide between monocotyledons and dicotyledons; some grasses of tall herb communities have elevated shoot meristems and in many forbs of pastures all leaves originate at the soil surface.

Foraging for mineral nutrients

Most grasses are known to develop a network of fine roots and on this basis it might be predicted that precision of root development in a nutritionally patchy medium would be highest in monocotyledons. Reference to Figure 3 does not confirm this prediction. In fact, low precision of foraging in the monocotyledons

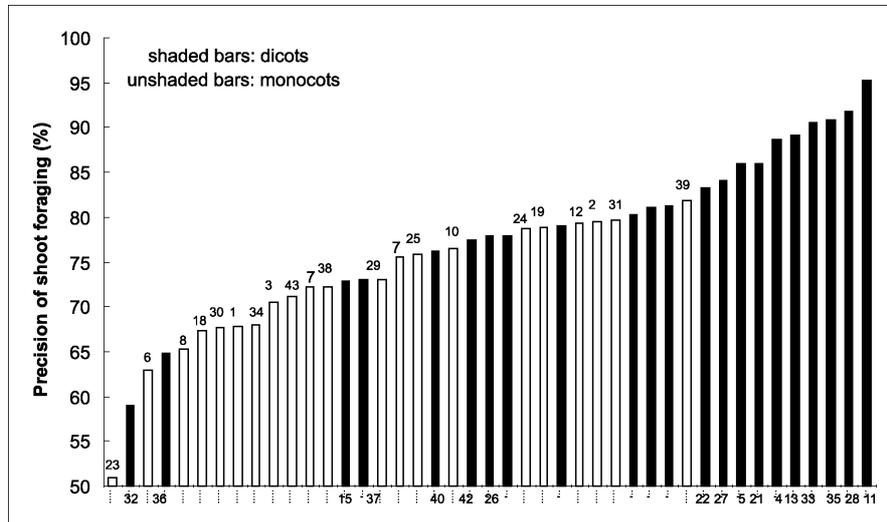


Figure 3. Comparison of 43 species with respect to the precision of root adjustment to the imposition of a nutritionally-patchy environment. A description of the methods is provided in Campbell *et al.* (1991). Species are identified in the legend of Figure 2.

is even more consistently observed in the roots than in the shoots. The most likely explanation for this phenomenon appears to be reliance of the monocotyledons on adventitious roots. Whereas the root systems of most dicotyledons have long-lived components from which finer roots continuously develop and track the changing patterns of resources, monocotyledons augment their root systems by producing fine roots independently near the soil surface. It is clear that this mechanism of construction involves considerable sacrifice of information concerning the local distribution of mineral nutrients within the soil. This raises a fundamental question as to the identity of the countervailing selection forces sustaining such an apparently inefficient mechanism of harvesting mineral nutrients. Here it may be important to recognise that in habitats exploited by vertebrate grazers, the persistence of turf-grasses involves not only frequent recovery of the leaf canopy but often also rapid reconstruction of the root system following trampling and poaching damage.

Conclusions

The early ecological conclusion that phenotypic plasticity, in common with genetic variation, has a primary significance in relation to the extent that it permits a widening of the niche breadth of some species is now giving way to a broader perspective. This recognises that plasticity is expressed continuously in all plants and for most of the time and is an integral part of the mechanisms by

which plants survive, capture resources, repel herbivores and pathogens and produce offspring. The challenge for ecologists is to develop a framework within which to classify the great variety of plasticity mechanisms. This short review has attempted to contribute to this process by focussing on the role of plasticity in resource capture and the conclusion has been drawn that this can be achieved by incorporating plasticity mechanisms into a framework of primary plant functional types. In particular it appears that the distinction between morphologically plastic responses and cellular acclimation has a profound significance in relation to correlated variation in a basket of other traits that determine the fitness of plants over gradients in habitat productivity and intensity of disturbance.

The large-scale comparative investigations of the precision of plastic responses of shoots and roots to resource patchiness, published for the first time in this paper, confirm the existence of patterns of variation that are useful predictors of the status of species in plant communities. It is apparent however that the precision of plastic responses by roots and shoots is subject to trade-offs against other properties (e.g. recovery from damage) which may be phylogenetically embedded.

References

- Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* **13**, 115–155.
- Campbell, B.D., Grime, J.P. and Mackey, J.M.L. (1991) A trade-off between scale and precision in resource foraging. *Oecologia* **87**, 532–538.
- Grime J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111**, 169–194.
- Grime, J.P., Crick, J.C. and Rincon, J.E. (1986) The ecological significance of plasticity. In D.H. Jennings and A.J. Trewavas (eds) *Plasticity in Plants*. Company of Biologists, Cambridge University Press, Cambridge.
- Grime, J.P., Thompson, K., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodgkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, M.A., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. and Whitehouse, J. (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**, 259–281.
- Lambers, H. and Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* **23**, 187–261.
- Larsen, D.W. and Kershaw, K.A. (1975) Acclimation in arctic lichens. *Nature* **254**, 421–423.
- Levitt, J. (1956) *The Hardiness of Plants*. Academic Press, New York, NY.
- Mooney, H.A. and West, M. (1964) Photosynthetic acclimation of plants of diverse origin. *Am. J. Bot.* **51**, 825–827.
- Reich, P.B., Walters, M.B. and Ellesworth, D.S. (1992) Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecol. Monogr.* **62**, 365–392.
- Strain, K.R. and Chase, V.C. (1966) Effect of past and prevailing temperatures on the carbon dioxide exchange capacities of some woody desert perennials. *Ecology* **47**, 1043–1045.