Consequences of the inherent developmental plasticity of organ and tissue relations

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Abstract. Varied cell lineages, random elements of stomata and vein patterns, and unpredictable details of branch relations are all examples of evidence for an inherent plasticity of development that need not be dependent on environmental cues. Such plastic form could be generated by a combination of programs and 'Developmental Selection', a principle that resembles Darwinian processes, albeit without genetic differences. Both internal and environmental cues could act by modifying the outcome of this selection. Adaptive responses to environmental heterogeneity cannot be strictly separated from the underlying plasticity of unperturbed development. The proximal mechanisms and the genetic specification of the outcome of developmental selection require an excess developmental potential, one that includes many unused alternatives. The choice between these alternatives depends on preset hierarchies, but this choice can be perturbed according to the environment as well as the internal conditions, including the ones due to random developmental mistakes. Form is specified as a balance between signals of the various components of the organism, without a strict determination of their precise numbers and locations. This requires that developing tissues and organs 'inform' the plant about their states and respond according to the signals and substrates they receive. Further, the varied responses must be integrated so as to form and maintain an organized, functional whole. Unexpected and unrecognized traits of known hormones, and especially auxin, suggest concrete knowledge about such mechanisms.
Plasticity that is based on developmental selection allows plants in a community to adjust their individual forms to those of their close neighbors. It could have important evolutionary consequences: mutations that have favorable effects on one process could be accommodated by plastic adjustments of other parts of the functional plant. On the other hand, genetic information required only for unusual conditions could be expected to deteriorate because it is not in constant use, and in fact plasticity that requires such is at best rare. At the conceptual level, plasticity calls for integrating reductionist and organismal thinking. A greater challenge is for the concurrent consideration of both proximal and Darwinian mechanisms.

Key words: apical dominance, auxin, branch competition, developmental selection, limits of plasticity, proximal and Darwinian mechanisms, redundant organs, regeneration

The adaptive domain of developmental plasticity and contiguous phenomena

I suggest that the question is based on a common intuitive paradigm, often implied rather than stated. Development is assumed to follow strict programs;

plasticity consists of switches between alternative programs in response to environmental cues. I will therefore use this question (ignoring some of its components) so as to point to a different way of looking at plasticity and, more generally, development. This is meant to be useful because it illuminates many ignored facts, not because it is mutually exclusive with more common views. The alternative paradigm of development may be introduced by considering an individual plant, growing in the uniform environment of an ideal growth chamber. The common paradigm might suggest that a plant in these conditions would express no developmental plasticity. Yet reality may not be that simple. The growth of the plant itself changes the environment of its individual organs, an obvious example being the shading of lower leaves and branches. Further, anything as complicated as the development of a plant could not proceed without 'mistakes', random events that could have large consequences. They must be reversed or development must continuously build upon previous events, including those that might appear to be random deviations. These points will be developed further below, but the conclusion can be stated in advance: adaptive responses to environmental heterogeneity are based on an underlying plasticity which is at the very heart of the proximal mechanisms of unperturbed development (Sachs, 1991, 1994, 2002, 2003; Sachs and Novo-plansky, 1995). This could go even further, stating that plasticity is characteristic of most aspects of biological organization, but the discussion here will be limited to the development of land plants.

So as to explain why plasticity is a basic characteristic of development it might be best to consider additional, related phenomena or processes, ones that are not mentioned in the question posed by the organizer. I will focus on three such phenomena: regeneration, the influence of a plant on the changing environment of its own organs, and the inherent random elements of biological development and mature structure. It is possible, of course, to define the commonly treated aspects of plasticity as separate phenomena, and such definitions can be quite useful. In answers to other questions, however, I hope to show that looking at underlying traits on which plasticity depends can contribute to understanding its mechanisms, roles, and origins. This view of plasticity contrasts with Diggle's answer, and differs from or complements Grime and Mackey's answer in its emphasis on proximal mechanisms rather than ecological adaptations. It is in agreement with Alpert and Simms (2002), in considering plasticity as a way of achieving homeostasis and with Schlichting and Smith (2002), though the topic is developed in a different way.

Additional processes related to plasticity

I will start with conclusions that can be had from observing regeneration. Herbivory and other damage are common environmental hazards. Plants are

certainly remarkable in their ability to respond by replacing parts that had been removed and thus renewing the balance between their various essential functions. Yet, contrary to common views, regeneration is quite restricted; it rarely involves developmental changes in mature, non-meristematic tissues. Instead, meristems, the organized tissues committed to continued development and organ formation, are present in great excess. Responses to damage depend on changes, or on a redistribution, of meristem developmental rates (Sachs, 1991). Such redistribution, however, occurs even in intact, undisturbed plants: there is a continued modulation of each meristem according to the changing state and development of the rest of the plant. Each organ is therefore required to 'inform' the plant about its state, and to respond to the signals and substrates it receives. An obvious extreme expression of such correlative information is apical dominance (Cline, 1994; Aarssen, 1995), or the relative inhibition of the development of new organs that would carry out the functions of ones that are already present. This inhibition suggests that when any organ is removed the configuration of signals changes, and remaining meristems tend to increase their developmental rates (Sachs, 1991).

There is an important conclusion here. Regeneration need not depend on special signals and developmental systems, ones that have evolved specifically so as to deal with herbivory. Plants do react to the wounds themselves, but it is not the wound reactions that are involved in the replacement of removed organs. Instead, everything known points to regeneration being an expression of the very same controls that are required for unperturbed development (Sachs, 1991). Even where mature tissues do redifferentiate, as in the formation of vascular contacts around wounds, they are responses to the redistribution of the very same hormonal signals that determine the continued differentiation of vascular tissues in the intact plant (Sachs, 1981).

A second relatively neglected type of plasticity-related phenomena is a consequence of the continued development of individual plants. The relative role of each organ changes as the rest of the plant develops and the organ itself ages. The form of plants must be considered as a dynamic entity, one which requires constant adjustments. These changes are due to development occurring locally, in meristems, rather than throughout the plant. A common example: a new branch, formed at the top of a tree, is gradually shaded and dominated by younger branches. It is common for most of these shaded branches to die and be shed, even in a plant that has no neighbors; this is the way most bare trunks are formed (Sachs and Novoplansky, 1995). Pruning and experimental work on model annuals indicate that the death of the lower branches depends on communication between branches by means of the dominance signals, mentioned above. It is likely, however, that the environment of individual branches, influenced by the rest of the very same plant, is also an important factor (Snow, 1931; Novoplansky *et al.*, 1989; Sachs and

Novoplansky, 1995; Stoll and Schmid, 1998). The actual development of a branch depends on the integrated effects of the plant and the environmental conditions (Novoplansky *et al.*, 1989), including the conditions that are perceived by the phytochromes. A possible hormonal mechanism of this integration is discussed in answer to the third question, the one about the mechanisms of plasticity.

Two general suggestions follow. There are adjustments during development which are required and manifested even in isolated plants and in uniform environments (Diggle, 2002, discussion of Heteroblasty). Depending on definitions, they are either manifestations of plasticity or closely akin phenomena, likely to overlap in both evolutionary origins and mechanisms. A second suggestion is that the immediate environment of individual organs might be used by plants for dealing with the constant changes that are a necessary consequence of their own development, not only for dealing with neighbors, living and inanimate. Even phytochromes, the best known receptors of environmental information (Schlichting and Smith, 2002), might be required in the relations between the branches of the very same plant.

A third group of phenomena, akin to plasticity and yet not included in its common definitions, is the innate variability of unperturbed development. It is a fact that development is variable in no necessary relation to environmental heterogeneity (Sachs, 1994). For example, the precise locations of branches vary a great deal, even independently of the local environment (Sachs and Novoplansky, 1995). This variation is also seen in vein patterns. At least at the time these are determined, in the leaf primordium (Sachs, 1981), their detail is much finer than environmental heterogeneity, and must therefore depend on internal events. Another example is seen in common garden chimeras, which in themselves are due to mutations and are thus outside the realm of plasticity. They do, however, indicate the course of undisturbed development: where one of the meristematic initial or stem cells is unable to form chlorophyll, all tissues formed by its divisions are albino and readily recognized (Tilney-Basset, 1986). The albino patches thus provide direct information about the cell lineages – and these lineages vary a great deal, even when the two halves of an unperturbed leaf are compared (Stewart and Dermen, 1975). These examples are by no means unique; they are expressions of phenomena found in all complex organisms and at all levels of organization (Sachs, 2002). Though quantitative comparisons have apparently not been published, there are no indications that these variations are reduced in artificial, uniform conditions. There is, of course, a variability or asymmetry that may be increased by stress conditions (Møller, 1995), but there is no reason to assume that the underlying, common variation in the course of cell divisions expresses any stress conditions. A distinction between such innate variability and plasticity 'is difficult to maintain' (Bradshaw, 1965).

Developmental programs or 'developmental selection'?

Conclusions from the examples above can be taken a step further. The common paradigm of genes determining stages of a strict program or recipe of development can be misleading (Nijhout, 1990); it would not account for the general fact mentioned above, that development can follow many variable courses and yet reach a functional outcome (Sachs, 1994). An alternative, which may supplement rather than exclude developmental programs, is a specification of a balanced state of tissues and organs. For example: the supply of water and ions, a function of roots, must be balanced with the photosynthetic performance of the leaves, and *vice versa*. This is an expected 'outcome' of development, which in plants is a dynamic state, involving continued organ initiation, growth and replacement. The genetic specification of a balance of this kind need not be as mysterious as it might first sound. A thermostat can specify the temperature of a room, and yet it does not follow any program or precise course of events (Rose, 1997).

It is easy to show, furthermore, that a genetic specification of a balanced outcome could have a concrete molecular meaning. Again the relations between the shoot and root systems can serve as a simple example (Sachs, 1991). The shoot is the source of auxin, and presumably other signals, which enhance the initiation of roots. The roots, in turn, are the source of cytokinins which enhance the development of the shoot (Matthyse and Scott, 1984). The balance between these two hormonal systems should depend on hormone synthesis, which means that it depends on the activity of enzymes that are genetically specified. Enzymes are also needed to degrade the hormones once they have reached their target organs (Kerk and Feldman, 1995). Other proteins have roles in the canalized, polar transport of hormones (Sachs 1981; Gälweiler *et al.*, 1998). Of course no claim is being made here that this is the only control of the relations between shoots and roots (discussed further in answer to the question about mechanisms of plasticity). The point here is only how the balanced state of plant organs could depend on the nature and expression of genetic information.

In the absence of a strict program there must be developmental rules that assure attaining dynamic balanced conditions. This balance must be reached reliably from various states – following chance perturbations or mistakes that are bound to happen in any complex developmental processes, after severe damage, or when the local environment changes. Observations of plant development (Sachs, 1991, 2003) suggest that there is always a large excess developmental potential, that there are many unused developmental alternatives. For example: though the determinate growth of leaves would appear to depend on a strict program, early damage to leaf primordia leads to regeneration by enhanced, unusual growth of the remaining tissues (Sachs, 1988). It follows

from this regeneration that the potential for growth is far greater than that which is actually expressed in intact leaves. Another, more obvious, example is seen in the relations between branches. In most plants the number of buds greatly exceeds the number of branches that actually grow, and, as mentioned above, most of the branches that start growing in spring remain small and are eventually shed (Sachs and Novoplansky, 1995). The occurrence of any developmental alternative, however, inhibits similar developmental events elsewhere – a general principle whose most common expression, mentioned above, is apical dominance. It follows that the precise location of buds or branches that actually grow may be quite variable, and yet an overall balanced relation between branches and between the shoot and the root systems could still be reached.

The relations between branches, whose details and hormonal basis is considered in the answer to the question about mechanisms, can be thought of as a competition for a role in a balanced state, and it is this balance that is genetically specified. The same competition can be expected between other redundant structures, the ones that have the same physiological roles, such as roots, fruits, or vascular strands (Sachs *et al.*, 1993). This developmental or 'epigenetic' selection (Sachs, 1991, 2002) may be a way in which adapted form is repeatedly reached by a Darwinian-like mechanism, albeit without genetic differences. The specification required for such developmental selection might well be simpler and more reliable than any precise genetic information about the course of the development of individual branches or other organs. A result of developmental selection would be variable development, which is readily observed. The constrained variability associated with such selection need not have a serious price in terms of reduced function. Variability could even be necessary for reaching balanced states and for avoiding getting trapped in suboptimal solutions, or balanced relations that represent local rather than overall optima (Gell-Mann, 1994).

The variable course of development, at all levels, can be considered a form of plasticity. It is presumably more amenable to quantitative modulation, both during ontogeny and during evolution, than any development that would be specified as a strict program. Developmental selection should also permit responses to local environmental conditions and to the general vigor of the plant that need not require special processes and special genetic information. This suggests that there could be many expressions of developmental plasticity that need not require the selection of special genes (Via, 1993), even if their occurrence is essential in other cases (Schlichting and Pigliucci, 1993).

How is plasticity related to other phenomena?

What, then, would I suggest about the relations of phenotypic plasticity to the phenomena listed in the question posed by the organizer? Dealing with addi-

tional, related phenomena not mentioned in the question and their proximal mechanisms suggests that plasticity does not occupy a defined, separate domain. Definitions which limits plasticity to responses to environmental cues can be misleading, therefore, focusing on overt adaptive aspects and ignoring the underlying mechanisms. The overlap between phenomena is larger than was indicated in the question. Furthermore, this overlap is real, not a function of confused conceptual thought. The need to define is ours, and I submit that it is not always fruitful (Sachs and Novoplansky, 1995). It is still essential, of course, that one be precise about an *ad hoc* definition that is used in any given discussion; it is only the hope for precise definitions of broad concepts that should be given up. Any system of definitions that would resolve some conflicts would result both in raising others and in a loss of useful concepts.

I would avoid a definition, but the discussion above does point to a characteristic that goes beyond differentiation and metamorphosis. Plasticity includes processes and events that are alternative ways of reaching what could be essentially the same functional result. These alternatives can be used for adaptive responses to varied environments, but their full understanding can be expected to require their underlying developmental mechanisms. In answers to other questions I hope to show that this view leads to significant suggestions about the origins and roles of plasticity.

Types of developmental plasticity

In the answer above I suggested that plasticity can be viewed as a characteristic of organization and development. It enables a plant to adjust, both structurally and physiologically, to its own development and to the habitat it happens to be in. It therefore maximizes performance. My answer to the present question, similar to Schlichting and Smith's (2002), is that whether this plasticity results in stability or flexibility in different environments depends on the parameters used for the comparison. The problem raised would than be due to an emphasis on one criterion for plasticity, its adaptive value as expressed by seed mass in one or a few years. Judging plasticity only by this criterion ignores the 'details' that point to its proximal mechanisms, constraints and variations.

The same would be true, of course, of animals, and similarities are pointed out in Grime and Mackey's answer. Three differences, however, are suggested by the ways plants and animals are organized and the ways they function. These differences are important in themselves, and they also emphasize characteristics that enlarge the view of plasticity suggested above. Both plants and animals, however, are extremely varied, and any complete treatment is likely to include a boring list of reservations. For the purpose of pointing to principles the following discussion will be limited to a broad comparison of

developmental plasticity in some large mammal and an herbaceous Dicotyledon. Their underlying living machinery is very similar, and their ways of making a living remarkably different. How does this affect their developmental plasticity?

A key characteristic is the way plants develop, the formation of new organs throughout their life. This continued embryonic activity is the same point made by Alpert and Simms (2002), that plants are modular and indeterminate, but the stress here is on continued modification of plant organization. It is obvious that continued embryonic activity leads to greater possibilities for developmental plasticity in plants than in mammals. These possibilities include types of plasticity that are characteristic of plants: organs are often replaced according to changing conditions and the variation in the size of a given plant, probably the most obvious and common expression of developmental plasticity, is much greater than any corresponding variation in animals.

Land plants, furthermore, must absorb energy and essential substrates through shoots and roots, which are different, complementary organs. Animals, in contrast, rely on food that enters through one mouth. Since the environmental heterogeneity above and below ground need not be closely correlated, plant organization requires a plasticity in the relations between organs. This plasticity is of a kind or at least a degree that is quite unique.

Finally, a third related point is that plants have many redundant organs, ones that have the very same functional roles (Sachs *et al.*, 1993). Obvious examples are leaves, branches, roots and flowers. Each type of organ can differentiate to have partially or wholly complementary roles (Stuefer *et al.*, 1996; Alpert and Simms 2002), but it is also common for organs to be redundant, to carry out the very same physiological processes. Coordinating the number and longevity of these organs requires principles of organization that are special to plants. The corresponding plasticity is at the organ rather than whole plant level (Novoplansky *et al.*, 1989).

Mechanisms of developmental plasticity

Experiments, and especially laboratory experiments, emphasize defined conditions in which very similar situations can be compared. Research along these lines characterizes algorithms, chains of events that determine a causal relation between a specific difference in the environment and a plant's response. Exciting results, using molecular techniques, are unraveling the precise details of such algorithms (Taiz and Zeiger, 1998; Schlichting and Smith, 2002). Responses to defined cues have also characterized many important types of plasticity (Silvertown and Gordon, 1989). These responses however, are building blocks of more complex situations which are common in natural, ecological conditions. Mechanisms of responses to individual cues can be expected to be organized or

coordinated so as to take into account the complexity of the conditions faced by an individual plant (Chapin *et al.*, 1993). Some of this integration can be at the level of gene expression (Schlichting and Smith, 2002; Givnish, 2002). My emphasis will be on a complementary higher level, that of the hormonal relations that could help integrate the development of the plant as a whole.

Three challenges of integrated responses

Little is known about how individual responses to defined cues are organized in real ecological systems. It can be suggested, however, that this organization satisfies the needs for integration of information and responses at three different levels. (a) Plants must develop according to all aspects of an environment, not any one of its components. (b) The internal environment – the age of plant, the age of the responding organ, and the presence and states of other organs of the same plant – must also be taken into account (Sachs *et al.*, 1993). (c) Developmental changes of any given organ should be coordinated with appropriate modifications of other varied parts, so that the plant remains a balanced, functional whole. Coordination is not used here in relation to ways in which different traits change (Diggle, 2002) but rather in relation to the different changes within the individual plant.

   Mechanisms that could meet these three requirements appear a tall order. Their study does not seem suited to reductionist research strategies. My purpose will be to show how the needs for integration might be met, especially by available facts about plant hormones (Chapin *et al.*, 1993), discovered on the basis of quite different and not necessarily correct hypotheses (Sachs, 1991). Such attempts at a synthesis of principles of plant organization should be of interest in themselves and it could also serve to raise questions and possible directions for molecular and cellular research.

Examples of experimental evidence

Snow (1931) performed seminal, early work on the effects of environmental conditions on branch growth. The unique aspect of his experiments was the combination of environmental conditions with internal relations between branches of the same plant. Only relatively recently has his work been repeated and extended (Novoplansky *et al.*, 1989; Sachs and Hassidim, 1996), and its implications are far from being exhausted. Snow developed a model experimental system, pea seedlings with only two shoots, each of which could be subjected to different treatments and environments. In the conditions he used small differences between the shoots tended to increase – only one of the two grew while the other was inhibited and eventually died (Sachs, 1966). The roots and vascular system developed so they supplied the successful branch.

Which of the two branches 'wins' and continues to develop? Success is influenced by preset hierarchies, which could act as default alternatives: thus the lateral shoots would not have grown in Snow's experiments if the original seminal shoot had not been removed. Success can also be influenced by the previous performance of the individual shoots (Novoplansky, 1996a). Further, the local environment can have a dominant effect: a shoot that is in a preferred situation (Novoplansky *et al.*, 1989) or has not been damaged (Sachs and Hassidim, 1996) has an advantage, and is the one that is most likely to grow. Relative success leads to one shoot inhibiting the development of the other shoot and gradually taking over an increasing role in the developing system.

The fate of a shoot was thus influenced by integrated information about its own state and that of the rest of the plant. This need not be true in all plants and conditions; plants are often assemblies of relatively independent modules whose activities are poorly integrated (Schlichting and Smith, 2002; Grime and Mackey, 2002). Results concerning plants with few shoots, however, do suggest that the integration between organs may be sufficiently concealed to be expressed only by controlled experiments. A concrete example was found in *Onobrychis* (Novoplansky *et al.*, 1994; Novoplansky, 1996b). As long as the plants were intact branches were autonomous, responding independently to local environmental conditions. Damaged and regenerating plants, however, showed that various branches were still capable of communicating and affecting each other's development.

Work carried out on other systems and topics after Snow's original experiments suggests a possible integrating mechanism. A growing branch is known to be the source of the hormone auxin (Went and Thimann, 1937). This auxin has varied effects on the development of the rest of the plant: it is a signal by which a branch inhibits the development of other branches, it induces the differentiation of vascular tissues oriented towards its source, and it enhances the initiation of new roots (Sachs, 1991). It thus integrates the different responses of the plant. Evidence that auxin does, in fact, determine developmental processes comes from precise measurements of auxin concentrations, but these are difficult and the available information is limited (Uggla *et al.*, 1998). Concentration at a given time, furthermore, is not the only parameter to which the tissues could respond. Various effects appear to be quantitatively related to the flow of the auxin, from its origin in the shoot tissues to the rest of the plant (Sachs, 1981, 1991). Flow is much more difficult to measure than concentration, but some quantitative information of the effective internal auxin can be had from vascular tissues differentiation (Sachs, 1981). This information supports the possibility that auxin flow depends on the rate the branch develops as well as on its local environment. The development of a branch situated in strong light, for example, is correlated with a greater and more rapid differentiation of its vascular contacts with the rest of the plant (Sachs *et al.*, 1993).

These facts lead to a suggestion that may seem surprising. Auxin appears to have a role in all three types of integration raised above. Its formation integrates various environmental conditions, it also depends on the developmental state of the organ in which it is formed, and, finally, the responses auxin elicits integrate varied changes in the entire plant. This sounds too good to be true. It is logical, however, and does fit available facts. Integration at various levels might well be the central role of auxin in plants (Sachs, 1981, 1991, 2000; Berleth and Sachs, 2001).

Other hormones and other possibilities

Auxin is not unique, neither in its dependence on many environmental conditions nor in its effects on varied developmental processes. Of course, the hypothesis that hormones play a major role in integration at all levels (Chapin *et al.*, 1993) goes much further than available evidence could prove. But it does seem a promising approach, suggesting experiments and measurements that could help bridge the gaps between developmental and ecological work. Perhaps the best evidence for another hormone having a similar role concerns abscisic acid. It is known to be formed in response to varied types of stress. This suggests that it might be a component of a mechanism that summarizes or integrates these stress conditions (Chapin *et al.*, 1993). The effects of abscisic acid are also not specific to any one plant response (Taiz and Zeiger, 1998), and the sum of their effects can be understood as preparing the plant for future stress conditions (Leshem and Kuiper, 1996).

The emphasis here on hormones as vehicles of interactions between an organ and the rest of the plant ignores other possibilities. The one most often considered, and even taken for granted, is that organs act as sources and sinks for essential substrates (Diggle, 2002). This suggests that interactions could be mediated by the exchange of the substrates required for continued development: sugar must be transported from the shoot to the root and various ions must move in the opposite direction. Mathematical modelling has shown that source/sink relations could even account for the regeneration following the removal of organs of one type (Thornley, 1972). For this to be true one must assume that transport can limit the distribution of substrates present in limiting quantities, restricting them to the organ in which they were formed or absorbed.

Since the exchange of substrates certainly occurs, source/sink relations appear to be the simplest possible mechanism. Any assumption of additional more complicated mechanisms, such as ones that include hormonal signals, requires evidence of unexplained phenomena (Wilson, 1988). Wilson's challenge, however, can be readily met. The following are three examples of common facts that could not be explained by source/sink relations:

(1) Seedlings, new plants developing from cuttings, and plants developing from storage organs (such as a potato tuber) grow for long periods at the expense of stored reserves. These new plants can often be maintained for 2 weeks or longer in the dark and in humid air, conditions in which their shoots and roots are not sources of any substrates. Yet such plants do maintain a balance between the two organs types, and regenerate this balance readily following severe damage.

(2) Shoots and root development is only most obvious expression of the balanced relations between the different parts of a plant. Another essential expression of these relations is the differentiation of oriented, canalized vascular channels (Sachs, 1981, 1991, 2000). There is no evidence that vascular differentiation can be induced by the substrates they transport once they mature, nor is there any mechanism by which this induction could occur. On the other hand, all aspects of vascular differentiation are induced by known hormones, and specifically by auxin (Sachs, 1981).

(3) Bacteria (*Agrobacterium tumefaciens*) genetically engineer plant cells to become unregulated sources of auxin and cytokinins (Taiz and Zeiger, 1998). This results in the formation of a tissue that is a sink for all substrates and a source of hormones. This tissue develops rapidly, competing with and inhibiting shoot development, becoming a large tumor (and a home for the bacteria, which cannot move in the plant). Further, genetic modifications that change the balance between the two hormone types result in the formation of teratomata in which organs of only one type are formed, with no relation to organ function. A local, exogeneous application of auxin and cytokinins in varied relations has the same effects. These facts could not be accounted for by any source/sink hypothesis that depends on organ function.

Hormones might be important because they have two roles that substrates cannot fulfil. The first is that hormones can act before and independently of actual substrate acquisition and use. This means that they can be formed in a developing organ before it is functional, and they can be affected by environmental signals (such as the photoperiod) before the environment actually changes. Hormones, therefore, can 'predict' the future. The second major role is that hormones can be organ and tissue specific. For example, the very same substrates are needed for root and shoot development, and auxin, for example, can enhance one and inhibit the other. At the same time auxin induces vascular differentiation, thus serving an essential integrating function for plant organization.

Relation to ontogeny

It is now possible to suggest an answer to the second question, how mechanisms of plasticity vary with ontogeny. Plants must respond to various sources

of information, and a major one is their own size, or the development they have undergone. It is obvious that this information is of considerable ecological significance (Lacey, 1986), and it is not surprising that developmental changes with age are common, examples being the transition to reproductive development and Heteroblasty (Bernier *et al.*, 1981; Poethig, 1990; Diggle, 2002). There might well be less obvious physiological changes with age (Nougarède *et al.*, 1989).

The transition from the juvenile to the mature state is often gradual (Chouard and Aghion, 1961). Some information accumulates in the apices, and it is most closely correlated with the number of leaves (and hence also nodes) they have formed (Paton, 1978). Rooting cuttings and grafting apices in unusual locations demonstrate that what is 'measured' are some physiological distances to the roots (Crone and McDaniel, 1997). Further, the information about these distances accumulates over time (Sachs, 1991). Whether this is to be considered a plasticity or not is a matter of definition. There is no doubt that plant responses depend on interactions between environmental cues and their physiological age. For example, the intensity of photoperiodic induction required for flowering of peas can be a function of plant age expressed by the number of leaves it had formed (Reid and Murfet, 1977).

The developmental changes with age occur in individual apices and modules rather than at the level of the whole plant (Ryleski and Halevy, 1972; Sachs, 1991). This is a fact that is often ignored. Small basal branches can be juvenile, can behave the way young plants do, even where the large axes are mature and reproductive (Sachs, 1999). Depending on environmental conditions a plant may divert substrates to apices that are in different ontogenetic stages, and this could be an important basis for developmental plasticity.

Conclusion

The nature of the essential integrating mechanisms required for environmental information and plant responses can now be stated in more general terms, independent of hypotheses about roles of plant hormones. The data supplied by environmental cues must be processed, extracting some quantitative values that reflect the totality of their interactions, a totality interpreted according to the age of the plant and its evolutionary experience. Such data processing could occur if the various effects of the environment acted on some central controlling element. This control should also be influenced by the internal correlative effects of the various plant organs. The very same controlling element must, furthermore, act to change plant development. Directly or indirectly it should influence the different parts of the plant, assuring the maintenance of integrated function and therefore of a balance whole. We commonly think of such data processing and integrated responses as a function

of nervous systems, and the absence of nervous systems in plants makes the questions raised here all the more interesting. There is good evidence for the suggested answer, involving the synthesis of and responses to few key hormones. This only means that it is likely to be important, certainly not that it is the only answer.

Consequences of developmental plasticity for higher organizational levels

In answers to previous questions I tried to show that plasticity can be viewed as a general characteristic of biological development. It is expressed at all levels of an individual's organization, including the relations between its organs. The inherent plasticity of development can have important consequences for the ways a plant adapts to being part of a community and to an heterogeneous environment. My answer to the present question will therefore emphasize relations between organs rather than whole plants, and will be different and complementary to those of other participants. Two examples should suffice to indicate the potential of the approach I suggest. The first concerns the adjustments of the form of individual plants to the presence of their neighbors and the second to adjustments to the temporal and spatial heterogeneity of the inanimate environment.

Organ plasticity and plant packing

The plasticity of organs could have a major role in the relations between neighboring plants. For example: plants generally have larger branches on the side that is less shaded (Novoplansky *et al.*, 1989; Stoll and Schmid, 1998; Henriksson, 2001). As a result, a strong neighboring branch can divert branch growth in other directions. Roots branch preferably where essential ions are available (Drew and Saker, 1975), and this could often be where there are few neighboring roots. As in the shoot system, root branching in one location is likely to be at the expense of another (Gersani and Sachs, 1992). In general terms: developmental plasticity enables an individual plant to adjust its form to the details of its immediate, heterogeneous environment.

It follows that organ plasticity should enhance a closer packing of neighboring plants, of both the same and of different taxa. Such packing should have consequences for community organization. It could matter most where environmental heterogeneity is on a fine scale, that of the individual plant. This is often a result of biological competition rather than the physical environment. Thus an effect on plant shoot packing should be most important where vegetation is dense enough so that the various shoots impinge on one another.

Plasticity in different niches

In many habitats plant density is low, being limited by the availability of water or other resources. In the absence of neighbors the environment of the individual plant would tend to be relatively uniform and organ level plasticity can be expected to have a limited effect. Thus organ plasticity may suggest another reason for Grime and Mackey's generalization, that in conditions of environmental stress developmental plasticity is relatively low (Grime and Mackey, 2002).

Even in conditions of low plant density the local environment can still be heterogeneous, of course, both in space and time. The following example is meant to illustrate conceptual problems concerning species differences in the responses to such heterogeneity. In a desert or a relatively dry environment a rain may mean different things, depending on the chances of its water being stored locally and the chances of following rains (Aronson *et al.*, 1992). The response of the plants depend on having some information, often accumulated by evolutionary experience, about the meaning of such rains and information about an actual rain has different meaning depending on the plant species and its adaptations. Desert *Cactaceae*, for example, rapidly form thin absorbing roots in response to a single rain event (Kausch, 1995). The price in substrates of forming such roots, whose life expectancy is short, must be relatively low. The value of these thin roots is correlated with the limited yet real water storing ability of the *Cactaceae* and, especially, their greater water use efficiency, as compared with most other plants (Kluge and Ting, 1978). The information that water will be available for a few days, which is of little use to most plants, is thus meaningful for the *Cactaceae* way of life. I submit that the question whether these plants are more or less plastic requires definitions and restrictions and may not be amenable to simple generalizations. Often it is only at the level of specific developmental processes, such as lateral root formation, that the plasticity of the responses of different plants can be compared.

Developmental plasticity and evolution

What plasticities have not emerged, and why?

Many expressions of plasticity could be missing because of their costs, including the ones that are only indirectly related to any adaptive role. Such costs have been discussed by deWitt *et al.* (1998) and they are treated in other answers (Alpert and Simms, 2002; Diggle, 2002; Givnish, 2002; Grime and Mackey, 2002). Another possible reason for missing expressions of plasticity is that their evolution would require unlikely, maladapted intermediates. With

some overlap with Schlichting and Smith's answer, I would like to use this question to point out a third kind of missing plasticity. This plasticity would depend on genetic information that is actually available and used for other purposes. Its potential adaptive role seems highly likely. I will suggest an important and often neglected reason for its absence.

It might be best to explain the phenomena I have in mind by considering an extreme, imaginary case. Individual plants often have juvenile and mature phases that differ in many traits. In *Hedera helix*, for example, the juvenile phase is a climber and the mature one a bush (Sinnott, 1960), and they would be difficult to identify as belonging to the same genus if they were not so obviously parts of the same plant. *H. helix*, furthermore, is by no means unique; dramatic changes in form during the life of a plant are the rule rather than the exception (Poethig, 1990; Diggle, 2002). Even more dramatic differences can be seen between the gametophyte and sporophyte phases, both photosynthetic, of mosses and ferns. Why are comparable differences not common responses to local environmental conditions?

Plants with specialized forms adapted to different environments would have the best of two or more contrasting worlds: they would be broad generalists in terms of the environments they could exploit and would still be highly specialized in their local adaptations. Many of their seeds would fall in appropriate locations. It might appear that there should be no problem about the evolution of such plants, ones adapted to very different environments. It is easy to conceive of a juvenile form that would form flowers directly, once it has grown large enough in a specific environment: these would be shifts in the relative timing of reproductive development (heterochrony), shifts that are known to occur fairly readily, in response to point mutations (Yang *et al.*, 1995). Similar heterochrony, though in the opposite direction, could make a mature form develop directly from the germinating seed in other, appropriate, conditions. Both changes would require no additional genetic information, other than that needed to sense the environment, since the forms required are already specified in the different phases of the life of the same plant.

Thus the general question: why is it not common for plants to have a number of different forms and physiologies, highly specialized for coping with local conditions in each of a range of different environments? Of course plants with specialized submerged leaves do occur (Sinnott, 1960; Bruni *et al.*, 1996), but they, too, are limited to situations in which each plant is likely to have both types of leaves. Species with distinct individuals in dry and submerged conditions are at best uncommon.

I suggest that the contrast presented above, between differences of life cycle phases and differences associated with phenotypic plasticity, is not readily explained by available hypotheses about the costs of plasticity. This contrast is also not explained by any adaptive limitations of intermediate evolutionary

states. An additional reason limiting plasticity could be the deterioration of any genetic information that is not used and repeatedly selected in most if not every generation. Though DNA is remarkably stable and its copying mechanism is reliable and subject to proof reading, mistakes (or mutations) always occur. Modeling has suggested that this could be important enough to be a major reason for the prevalence of sexual processes throughout the biological world (Michod and Levin, 1988). Such deterioration of genetic information is countered by constant selection: this is needed not only to increase the frequency of rare promising variations but also to weed out common mistakes. It is here that a limitation specific to plasticity could come in, one that would not be expressed in different phases of life cycles. Specializations for different environments would require information that would not be used in every generation, and might therefore be subject to rapid deterioration. Such deterioration would not occur where the differences appear, and are subject to selection, during the life cycle of each individual, as they do in the juvenile and mature phases of *Hedera* and other plants. Experimental support for this suggestion is available from work with a unicellular organism, *Chlamydomonas*. Reboud and Bell (1997) found that selection for generalists is enhanced more by the deterioration of information than by the prices of specialization. The evidence was that generalists could be readily selected by an environment that varied in time but not by one that varied in space.

Neglected influences on the course and rate of evolution

There are commonly discussed answers to this question, and they need not be reviewed here. The general picture which was outlined in relation to previous questions, however, was that plasticity can be viewed as a basic trait of developmental systems, not only of responses to environmental conditions. The following two points, though not new, derive from the ways such systems could evolve. Another reason for their being mentioned here is their potential contribution to the ways inherently plastic development could function.

Both experiments and theory show that mutations are likely to result in an unbalanced, poorly organized system. For example: a change increasing the function of photosynthetic tissues would be advantageous only when accompanied by changes in the function of the roots, needed for the increased supply the water and ions. It is extremely unlikely that the necessary mutations would occur together at the appropriate time. It is here that plasticity could come in: a demand for substrates absorbed by the roots is translated into signals that enhance root development, and the new system can be balanced the way it would be during regeneration (Sachs, 1991). In more general terms: internal plasticity should provide adjustments to mutations that affect only one component of a complex system (Schmalhausen, 1949). This should reduce the

negative effects of mutations by preserving overall, integrated function. In the long run there could be a selection of modifier genes that would provide constitutive adjustments of the various functional systems of the organism.

Another side of the same coin is that a developmental plasticity should accommodate or correct for the potentially deleterious effects of mutations. This means that many mutations need not be expressed by the phenotype, and thus need not be subject to selection (Schmalhausen, 1949; Schlichting and Pigliucci, 1998). Their effects might be uncovered under extreme environmental conditions, as in Waddington's (1953) genetic assimilation experiments. Under most other conditions plasticity would act to maintain homeostasis (Alpert and Simms, 2002). The example used above is appropriate here too: a mutation that increases one function at the expense of others would be masked by plasticity and could be preserved until other modifications make it advantageous. It follows that the plasticity of the developmental system would allow for a hidden genetic variability. This is, of course, analogous to the effect of diploidy. Only recently has the potential importance of such hidden variability been considered in any detail (Schlichting and Pigliucci, 1998).

Strategies in studying developmental plasticity

At present there is little cross-fertilization between the different valid approaches to plasticity. In agreement with other answers to this question I think it is obvious that combining different approaches could be a major way of promoting the study of plasticity. Further, there is conclusive evidence that the molecular approach to developmental mechanisms and environmental responses cannot be rejected. This is true even where the integration of information is not necessarily at the level of the genes (see answer 3). In trying to account for the relative absence of research that combines different levels I would point to two conceptual problems. The first is that any biological problem involves both proximal and Darwinian, or ultimate, mechanisms. The second problem, or apparent problem, is the contrast between reductionist and organismic or holistic attitudes. Neither of these is unique to plasticity, but they should be considered here because they appear to divide its issues by insurmountable barriers. Of course, much has been done by finding answers to defined questions at a single level or approach. I submit that this is not the most promising research strategy, and that synthetic ways of thinking have already emerged. These suggest that in the future we must be more ambitious and do what would appear to be almost impossible, using rather than accepting the apparent conflicts of the different approaches. So as to be as clear as possible I will deal with the two conceptual problems separately, though they certainly overlap.

Reductionist vs. organismic thinking

I will start with the separation that is less real, the apparent conflict between reductionist and organismic ways of thinking. Many of the arguments concerning this dichotomy arise from a confusion between reductionist research strategies and reductionist philosophy, which suggests that any trait can be derived from a lower level, from its building blocks. The emergence of new, essential traits that depend on but are not present in component processes is real and cannot be ignored. An example is the Darwinian mechanism itself, which is not present in its components, the processes of mutation and selection. There is no conflict between these statements about emergence and the fact that the dissection of components of complex processes has led to profound advances. Certainly not with the fact that reductionist research strategies are extremely powerful, probably because they are suited to our limited abilities of analysis and conceptualization. Experiments are always aimed at a reduction of a complex situation, and this includes natural experiments, ones that are found rather than preformed; and it is rather difficult to think of biology, at any level, without the experimental method.

For example: it was mentioned above, in relation to the mechanisms of plasticity (question 3) that the responses of an organism to the complex realities of the environment are more than the sum of the responses to single cues, ones that are readily studied in laboratory conditions. But even for dealing with the integration of internal and environmental information an illuminating approach was the reduction of this complex phenomenon to a system that is as simple as possible, including defined experimental conditions and only the minimal number of organs, two shoots (Snow, 1931). Reductionist research must, of course, be supplemented by general theoretical synthesis, and it is here that so little has been done. This statement, however, need not divide the practice or the theory of plasticity in any serious way.

While reductionist research is often the best way of dealing with complex problems, its narrow application has led to mistakes. Thus, for example, in answer to the question about the mechanisms of plasticity I pointed out that the emphasis on well-defined single responses to auxin has delayed the realization of its role in plant organization. What was missing was an organisic approach, or a comparative study of the varied responses that are elicited by auxin. Another example, given above, is the emphasis on the sink/source distribution of substrates as a sole mechanism correlating the development of plant organs. Again, including additional relations between organs proves that hormones must be required. The definition of the simplest systems, therefore, can be misleading. The need for a broad comparative approach, however, does not invalidate any basic concepts of reductionist research.

Proximal vs. Darwinian mechanisms

In contrast, the gulf between proximal and Darwinian causes is real: here I disagree with Schlichting and Smith's answer to the same question. A statement of causes in terms of only one of the two types of biological mechanisms is always incomplete. It is an answer that satisfies some people while leaving others cold. The difference between the two is profound: while proximal mechanisms deal with events at the level of individuals, Darwinian theory is at the level of populations (Mayr, 1982). Dealing with one mechanism without the other is often illuminating, but this will always be a partial picture of a rich reality. It ignores essential interactions between proximal and Darwinian mechanisms, and these interactions are the very essence of biology. Proximal mechanisms or causes are not ones that would have been planned by an engineer: they are products of long 'tinkering' by Darwinian evolution (Jacob, 1983), an evolution that does not produce ideal results nor follow a reasonable short course. For this reason proximal mechanisms cannot be fully understood except in relation to their evolution: they are not necessarily optimal, and their logic may make sense only in an evolutionary context. The other side of the coin is that evolution is itself constrained and directed by available proximal mechanisms (Alberch, 1980). It is only by seeing both the proximal and Darwinian sides of any phenomenon that a complete picture can be had.

Acknowledgements

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