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Phenotypic plasticity: a useful framework for understanding adaptation in forest species

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Abstract

Phenotypic plasticity is a relatively new name for a very old issue in plant sciences: the ability of a genotype to generate a range of different phenotypes, depending on the environment. Contrasting with a great deal of published research works recognising plastic responses in a wide variety of organisms, direct evidences of the adaptive role of such responses are still scarce and the evolutionary implications of phenotypic plasticity is under discussion. Different types of plasticity, operating at different levels within individuals or across generations have been recognised and several methodologies have been applied to characterize and quantify plasticity. Further research on this issue regarding forest tree species, especially in Mediterranean ecosystems is needed in order to understand the impact that global climate change may have on the existing populations.

Key words: Phenotypic flexibility, Developmental plasticity, Cross-generational plasticity, Ontogeny, AMMI models, Stressful environments, Forest management.

Resumen

Plasticidad genotípica: un marco útil para entender la adaptación de las especies forestales

La utilización de la designación plasticidad fenotípica es relativamente reciente, sin embargo, es un aspecto muy estudiado: la capacidad de un genotipo de generar un amplio rango de fenotipos distintos según el ambiente en el que se desarrolla. En la literatura, se reconocen distintos tipos de plasticidad fenotípica, actuando a diferentes niveles del organismo o entre una generación y la siguiente. Además, se han descrito y aplicado varias metodologías para caracterizar y cuantificar la plasticidad. Sin embargo, es necesario profundizar en la investigación de este tema con relación a los árboles forestales, sobre todo en ambientes Mediterráneos, para poder entender el impacto que el cambio climático global puede tener en las poblaciones actuales.

Palabras clave: Flexibilidad fenotípica, Plasticidad en el desarrollo, Plasticidad trans-generacional, Ontogenia, Modelos AMMI, Ambiente estresante, Gestión forestal.

Introduction

Foresters and gardeners are fully aware that similar plants grown in different conditions may look very different. In fact, forest management has been using the control of micro-environment to shape trees into desired phenotypes for centuries. For instance, by modifying light, water and nutrient availability through variations in stand density, one can direct growth to build tall, branchless poles or alternatively to enhance crown development for seed production and subsequent stand recruitment. This ability of a genotype, i.e. of a single set of genes to generate a range of different phenotypes, depending on the environment that the developing organism must endure, is called phenotypic plasticity (Bradshaw, 1965; Schlichting, 1986). Phenotypic plasticity may take many forms, ranging from changes in physiology, to alterations of morphological structure and to shifts in behavioural repertoires (Schlichting and Pigliucci,

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1998). In any case, it is a property of specific characters in relation to specific environmental influences. Plasticity must be distinguished from differences that are not environmentally induced, but rather due to genetic differentiation among individuals or to fixed ontogenetic variation. Furthermore, some of the observed phenotypic variations are neither due to the environment nor to the genotype, but result from random developmental irregularities, i.e., from developmental instability (Bradshaw, 1965).

Research on Phenotypic plasticity started early in the twentieth century, but pioneer works have been largely overlooked, with some exceptions (e.g. Bradshaw, 1965). It was only on the last few decades that the scientific community regained interest in this concept (Sultan, 1987; Via, 1992; Dejong, 1995; Dewitt *et al.,* 1998; Agrawal, 2001; Hughes *et al.,* 2002; Schlichting, 2002; Sultan, 2005). Integrating the concept of phenotypic plasticity into biologic research helps to avoid oversimplifications such as the common idea that genes program development; organisms are increasingly viewed as developmental systems that continually integrate internal and external signals to modulate gene expression (Nijhout, 2003).

While initial studies on phenotypic plasticity often focused on simply describing the amount of morphological change observed in response to given changes in abiotic factors (most commonly light, temperature, water or nutrients), one of the major tasks nowadays relates to precisely interpreting to what extent do individual plastic responses to environmental variation enhance fitness in the environments in which such responses are expressed. Even if it seems clear that phenotypic plasticity must be recognised as central to evolution rather than a minor phenomenon, secondary to «real» genetic adaptation (Strand and Weisner, 2004), it is nontrivial to demonstrate that a variable response to a fluctuating environment is indeed adaptive. Demonstrating that the phenotype induced in a given environment has higher fitness faces significant problems because plasticity itself prevents the expression of non-responding or alternative less fitted phenotypes (Schmitt *et al.,* 2003), leading to the necessity of using manipulated genotypes or phenotypes (Schmitt *et al.,* 1995; Ackerly *et al.,* 2000).

In this paper, we intend to give an updated overview of some key aspects of research on phenotypic plasticity, with special emphasis in those issues more relevant to forest species. Hence, we have chosen some illustrative examples taken from the authors' research in forest species, complementary to the bibliographic review.

Types of phenotypic plasticity

In the widest sense, all the developmental process of an organism can be interpreted as the sum of all plasticity processes occurring at the cellular level, as a result of environmental changes occurring within and outside the cells through time (Schlichting and Pigliucci, 1998; Sachs, 2001; Sachs, 2002). However, for obvious reasons, plastic responses have been assessed at least at the organ or meristem level (De Kroon *et al.,* 2005), and more often at the individual level. There is some confusion about what should be considered «a genotype» for plasticity studies. While in a strict sense, the definition of phenotypic plasticity would imply the need to use clonal replicates, we often assume that a wider taxonomic entity will constitute a genotype in the wide sense, given it is repeatable. Hence, it is not unusual to work with families, populations, or even species (Schlichting, 1986).

Although numerous types of phenotypic plasticity have been termed in the recent bibliography on the issue, generating some controversy (see for example Piersma and Drent, 2003; Sultan, 2004), we have chosen to group them into three main, clearly distinct manifestations:

Physiological plasticity or phenotypic flexibility sensu Piersma & Lindstrom (1997)

There are countless examples of this type of plasticity in the bibliography, many of them gathered under the concepts of acclimation and acclimatization. These environment-mediated changes in physiological traits are, in most cases, reversible and constitute the basis of homeostasis at the individual level. Plasticity of a character is therefore equivalent to lack of homeostasis for that character; nevertheless, in many cases plasticity in an underlying trait contributes to homeostasis in traits more closely related to fitness (Alpert and Simms, 2002; West-Eberhard, 2003). Physiological plasticity is frequently analysed within each individual through the variation of a given attribute in time.

Developmental plasticity

Some organisms follow distinct developmental pathways in response to environmental cues by changing carbon allocation patterns. Specific adjustments can give rise to morphological and anatomical differences. This developmental plasticity is in most cases irreversible and often complementary to physiological, short-term plasticity (Givnish, 2002 and Fig. 1). Developmental plasticity is thought to be of key importance in plants, because of their limitations to mobility, lack of real «behaviour» and the continuation of development throughout the life of the individual (Novoplansky, 2002).

Cross-generational plasticity (Donohue and Schmitt, 1998)

This type of plasticity, better known as maternal effects, carry-over effects or genetic after-effects (López *et al.,* 2003; Galloway, 2005), can be briefly described as the shift in the performance of a progeny, caused by the maternal or embryonic environment. Although these complex effects have been little studied in plants, with the exception of several studies on the behaviour of genetically identical seeds produced at contrasted sites (Stoehr *et al.,* 1998), there is a recent, emerging interest on this issue in a more general context (Lacey and Herr, 2005). By contrast, it has been deeply studied in animals and there are also numerous examples applied to human health (see for example Bateson *et al.,* 2004 and references therein).

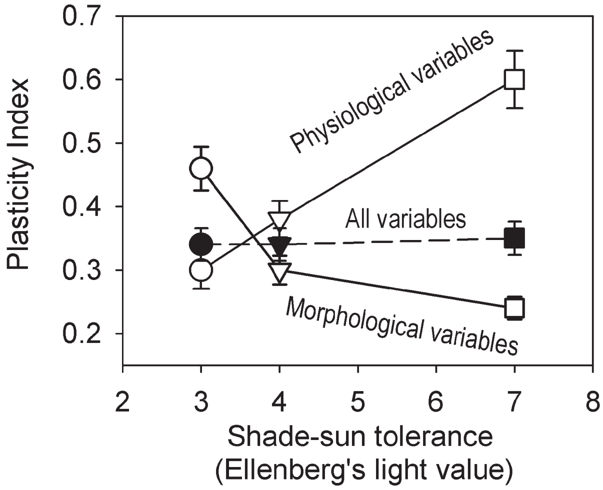

Figure 1. Forest trees significantly differ not only on the extent of their plastic phenotypic response to light, but also on the type of plasticity. Shade tolerant species tend to be more plastic in morphological traits while high-light species tend to be more plastic in physiological traits. In this particular case, when the plasticity index is averaged over all the variables studied, no differences were observed across species. Symbols: ○ *Fagus sylvatica* ∇ *Quercus ilex* □ *Quercus robur*. Modified from Niinemets and Valladares (2004).

Apparent plasticity

Quite drastic changes in morphology and in physiology often accompany plant development, such as those observed in the transition from seed to seedling or from juvenile to mature stages, but these ontogenetic changes represent the unfolding of a developmental programme where phenotypic plasticity may occur in the timing of the change but not in the change itself (Watson *et al.,* 1995; Alpert and Simms, 2002; Diggle, 2002). In many cases, developmental stage and environment alter the functional relationship between traits, as measured by shifts in allometric slope or intercept (Preston and Ackerly, 2003; Weiner, 2004). As a consequence, conclusions regarding phenotypic plasticity may differ dramatically if ontogenetic changes in phenotypic expression are taken in consideration (Huber and Stuefer, 1997; Müller *et al.,* 2000; Wright and McConnaughay, 2002). Separating these ontogenetic effects from truly plastic changes constitutes a central task of recent research on phenotypic plasticity (Sultan, 2004). The incorporation of size-related covariates in the models for analysis of variance or the comparison of allometric relationships between biomass compartments, so-called ontogenetic trajectories, help separating ontogenetic, size-related effects from true phenotypic plasticity (Poorter and Nagel, 2000 and Fig. 2).

When assessing developmental plasticity, there is an additional, relevant issue closely linked to ontogeny: the competence of the developmental system to respond at a particular moment in time (Schlichting and Pigliucci, 1998). The varied developmental pathways triggered by environmental events may be induced during sensitive, often brief, periods in development. Outside these sensitive periods (developmental windows) environmental influence that sets the characteristics of an individual may have little

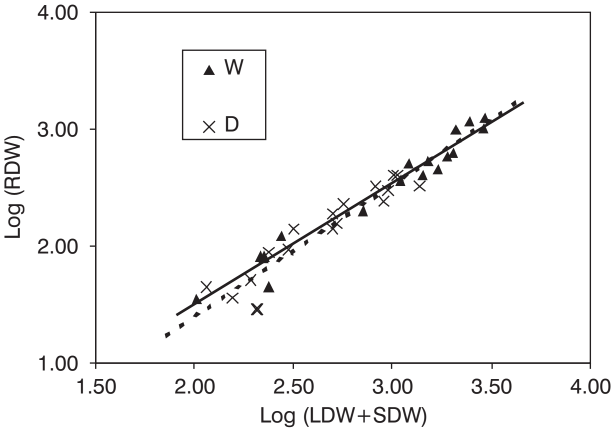

Figure 2. Comparison of linear regressions between ontogenetic trajectories of biomass compartments (log-transformed). RDW: Root dry weight; LDW: leaf dry weight; SDW: stem dry weight. In this case, well-watered (W) and water-stressed seedlings (D) of *Pinus canariensis* presented no differences in biomass allocation to roots when plant size (the sum of the other two biomass components) was taken into account, as shown by the overlapping lines. Nevertheless, both mean root dry weight and the ratio of RDW to total biomass were significantly different in this case due to size related effects. Elaborated from data by Climent *et al.,* unpublished.

or no effect (Bateson *et al.,* 2004). This apparently obvious, but often neglected requirement implies that an observed lack of plasticity for a given environmental stimulus could only be meaningful if the organism has the effective ability to respond at that precise developmental stage (Fig. 3). Similarly, phenotypic flexibility is not constant throughout ontogeny; the reversibility of a response varies over time (Piersma and Drent, 2003).

Adaptive plasticity

Phenotypic plasticity is not inherently adaptive; in some cases it might represent inevitable responses of the organisms that do not imply enhanced fitness (Wells and Pigliucci, 2000; Meyers and Bull, 2002). In fact, individuals raised under extreme environmental conditions usually present considerable phenotypical distortion (Bradshaw, 1965), often associated with reduced growth. In time these individuals may present very low reproduction rates and earlier mortality (Fig. 4). Although this behaviour must be considered an expression of phenotypic plasticity, in fact it reflects a lack of adaptation to that extreme environment.

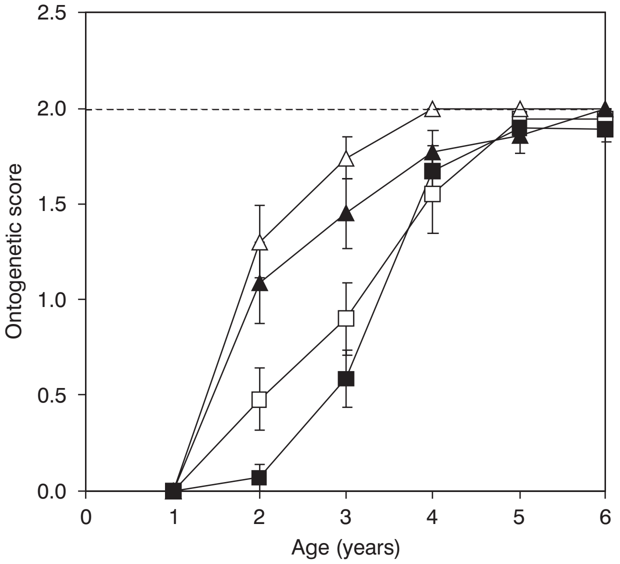

Figure 3. Evolution of shoot vegetative maturity, scored from 0 (juveniles with primary needles and free growth), to 2 (vegetative adult plants with secondary needles and fixed growth) for two provenances of *Pinus canariensis* (blanks: a northern wet provenance, black points: a southern dry provenance), planted at two contrasted sites (triangles: wet, fertile site, squares: dry, infertile site). Differences among provenances and sites can only be found at two and three years of age, while scant or null differences will be detected further on because eventually all plants will reach the vegetative adult condition. Therefore, between age two and three there is a «developmental window» allowing the assessment of ontogenetic differences in Canary Islands pine. However, the best picture of the process is obtained by comparing the complete trajectories: the onset of vegetative phase change, the slope from year to year and the offset of the process. Elaborated from data by Climent *et al.,* unpublished.

Quantitative estimation of phenotypic plasticity

Phenotypic plasticity is usually measured using an experimental design involving several replicates of the same genotype (or genetically related individuals such as clones or full-sibs, used in most studies on annual plants, or populations and even species when dealing with long lived plants or animals) distributed among a few ecologically meaningful environments. Often these experiments are conducted under controlled conditions, with the levels of only one or a few parameters being manipulated in a pre-determined way, to simulate an ecological gradient. Nevertheless, multi-locality common garden experiments, were the variability among environments is uncontrolled can also be used

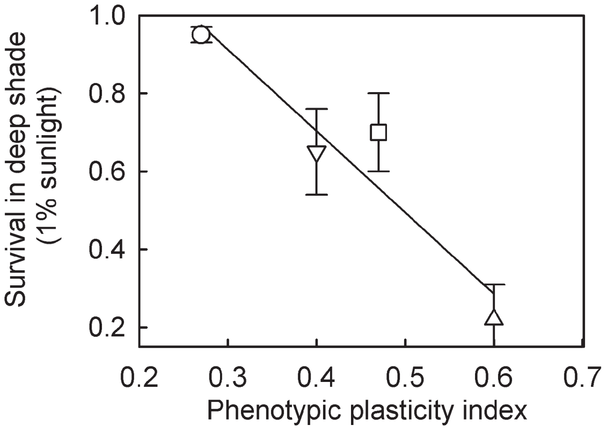

Figure 4. Phenotypic plasticity is not always adaptive. Elongation in response to shade, in this case quantified by an index of phenotypic plasticity from zero (null plasticity) to one (maximum plasticity), was linked to increasingly lower survival in deep shade in seedlings of four forest tree species *(Q. pyrenaica, Q. robur, P. sylvestris* and *P. pinaster)*. This differentially plastic response to light could lead to enhanced survival only when surrounding vegetation can be overtopped, which is not often the case in forest ecosystems. Symbols: ○ *Quercus pyrenaica* ∇ *Quercus robur* □ *Pinus sylvestris* Δ *Pinus sylvestris.* Elaborated from unpublished data of D. Sanchez-Gomez and F. Valladares.

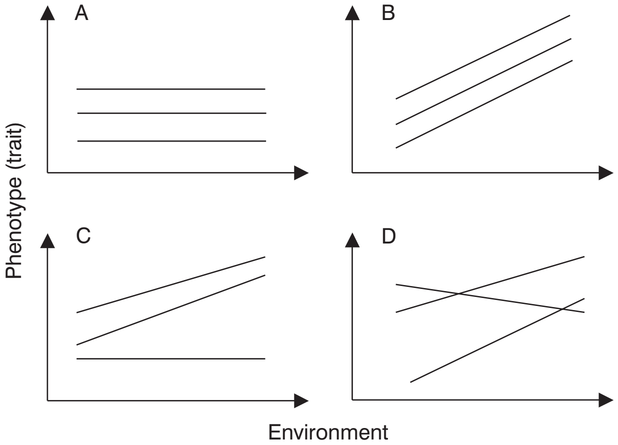

Figure 5. Conceptual graphical representation of reaction norms. Genotype means across environments are connected with a line, each line representing a different genotype. A: No phenotypic plasticity (denoted by flat reaction norms) but significant genetic effect (indicated by the distance between lines). B: Plasticity and significant genetic effect (sloped and separated lines) but no interaction (that is, all genotypes are equally plastic). C and D: Genetic differentiation for plasticity (differently sloped lines). Figure and text adapted from Dewitt and Scheiner (2004) and Strand and Weisner (2004).

for this purpose. From any of such experimental designs, we can build a function relating environmental input to phenotypic output: the reaction norm (Woltereck, 1909). Although the terms phenotypic plasticity and reaction norm are often used as synonyms, reaction norms are not always plastic (Schlichting and Pigliucci, 1998). Facing a given environmental change, phenotypes (traits) may either change or remain fixed, yielding in this case a flat reaction norm (Figure 5A). Graphically, the reaction norm can be represented in an environment / phenotype space, each line connecting the mean phenotypic value of a given genotype across environments (Fig. 5). In the simplest case, were only two environments are considered, this line is necessarily a straight line and the steepness of the slope indicates the level of plasticity for each genotype.

Although reaction norm diagrams are the most commonly used tool to visualize phenotypic plasticity, hypothesis testing is usually based on the partitioning of the observed phenotypic variation through analysis of variance into at least three components, genotype, environment and genotype by environment interaction. A significant environmental effect (Fig. 5 B) indicates that the character in question is plastic and a significant interaction term (Fig. 5 C and D) indicates the existence of differences among genotypes for plasticity (Schlichting, 1986). This method measures only the amount of phenotypic plasticity and the existence of variations among genotypes, without measuring patterns (Scheiner, 1993).

Several indices have been developed to quantify phenotypic plasticity when only two environments are being considered, most of them based on the difference between the average phenotypic values, frequently normalized by either the mean or the maximum value (e.g. Becker, 1964; Schlichting, 1986; Scheiner and Lyman, 1991; Via, 1994; Valladares *et al.,* 2000). A ranking of genotypes according to their plasticity can be obtained from any of these indices, but since most of them have no estimator of dispersion, statistical comparisons are not possible.

In any case, as responses to environment are generally not linear, the validity of studies based in only two environments relies on a very precise choice of the experimental conditions and generalizations are not always possible, nevertheless, the extension of those indices to more than two environments is not straightforward. Furthermore, when dealing with three or more environments, it is often more interesting to centre the analysis in the differences for plasticity among genotypes. Therefore, most authors suggested the use of analytical tools initially developed for the study of genotype by environment interactions (Schlichting, 1986; Scheiner, 1993). These methods are mainly focused in the identification of stable genotypes, in the agronomic sense of the term, i.e. genotypes that are able to maintain their productivity according to the potential of each environment (Becker, 1981), which is not equivalent to lack of plasticity. Therefore results must be interpreted under a different point of view.

The most commonly used method in this context, because of its simplicity, is the joint regression analysis, based on the linear regression of mean values of a genotype for each environment against the environment mean value of all genotypes (Finlay and Wilkinson, 1963). In this case, while agronomists would consider stable a genotype with a regression coefficient of 1, a non-responding genotype (stable form a biological point of view) would have a coefficient close to zero, higher values of this coefficient corresponding to higher levels of plasticity. This method poses two major problems: the assessment of environmental value is not independent from the genotypes being tested and the assumption of linearity of responses is not always realistic, leading to important differences among genotypes for the accuracy of plasticity measures (Fig. 6).

In the last two decades, the use of Additive Main effect and Multiplicative Interaction (AMMI) models (Gauch, 1988; Zobel *et al.,* 1988) for the study of genotype x environment interaction has become increasingly more popular for the study of adaptedness, mainly in crop plants. This approach incorporates both additive and multiplicative components into an integrated least squares analysis. The genotype and environment scores obtained from the AMMI analysis can be simultaneous represented into a biplot (Gabriel, 1971), allowing for a very clear interpretation of both differences in phenotypic plasticity and specific adaptation patters of the genotypes. One of the few studies where this method was applied to forest tree species (beyond a strict breeding context) is due to Wu and Ying (2001), who compared differences in phenotypic plasticity among several lodgepole pine provenances, obtained both with joint regression analysis and AMMI models. In this case, AMMI models, besides overcoming the dependency of the site and genotype indicators, as previously mentioned by other authors (e.g. Gauch, 1992), detected further differences among genotypes for plasticity that were undetected by joint regression analysis and yielded clearer patterns of adaptation of the studied populations to given sites.

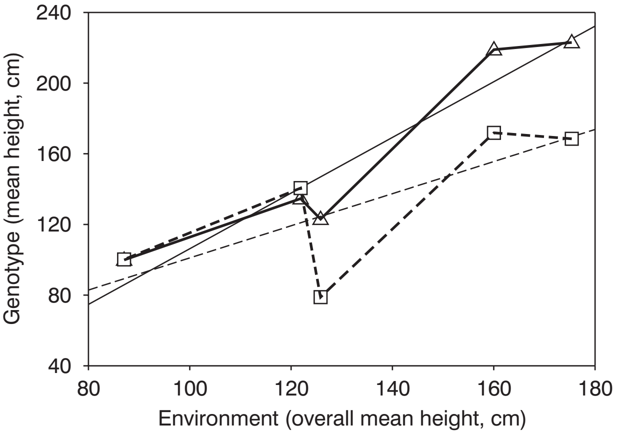

Figure 6. Norm of reaction and joint regression analysis for two genotypes (mean height of two populations of *Pinus sylvestris,* 8 years after planting) in the same set of environments (five distinct field locations). Genotype 1 (triangles and solid lines) has a close to linear response to the environmental variation (r^2 = 0.91), while for genotype 2 (squares and dashed line) the linear regression used to model genotypic response to the environment is far from the actual norm of reaction (r^2 = 58%) due to an extremely low growth in the third site, an average quality site.

Evolutionary implications of phenotypic plasticity

The idea that phenotypic plasticity constitutes a mere noise in the direct expression of a genotype and hence it is unimportant to evolution, dates back to the early XX century (Woltereck, 1909), but persisted well into the 1980s. Nowadays, even when there is an increasing agreement on the relevance of considering phenotypic plasticity in evolution studies, its actual evolutionary impact is still far from clear (Sultan, 2004). Authors, such as Schlichting & Pigliucci (1998) maintain that the focus of selective forces in nature is the capacity of organisms to deal with environmental contingency, rather than particular genes or discrete phenotypes. This is an extreme hypothesis, clearly opposed to Fishers' genetic determinism, and in fact other authors sustain that selection for plasticity is basically a by-product of selection for the best-suited phenotypes in each environment (Via, 1993; Via *et al.,* 1995), or postulated that most plastic responses must be first considered as «passive», leaving limited place for evolution due to costs and constrictions (Van Kleunen and Fischer, 2005). However, the idea of the costs for plasticity is mostly theoretical, and other empirical works have demonstrated that these costs may be greatly overcome by its benefits (Relyea, 2002; Dewitt and Scheiner, 2004).

Plasticity in limiting stressful environments

It is generally thought that adaptive phenotypic plasticity works against specialisation mechanisms, because if individual genotypes are sufficiently plastic to produce phenotypes appropriate to different environments, natural selection may not occur for genetically distinct, locally specialized ecotypes (Eriksson *et al.,* 1993; Sultan, 2000; Dewitt and Scheiner, 2004). However, differences in the environmental heterogeneity have been postulated to conduct to divergences in plasticity between the genotypes adapted to stable versus changing habitats (e.g. Balaguer *et al.,* 2001). Still, little is known about the trade-offs between plasticity and ecotypic differentiation in long-lived organisms that must face an environment that changes over time and space.

Developmental plasticity may be selected for when the state of the environment experienced by the developing organism is a good predictor for future environmental conditions and can therefore serve as a cue for an appropriate phenotype (Meyers and Bull, 2002).

A conservative resource-use strategy has been shown to be adaptive in adverse or limiting environments (e.g. Chapin *et al.,* 1993), and it has been argued that a reduced plasticity can be part of this conservative strategy. For instance, a reduced plastic response to light has been observed in true shade tolerant plants (i.e. those that not only stand very low light but complete their whole life cycle in deep shade) from tropical forests (Valladares *et al.,* 2000), and a limited responsiveness to either light, nutrients and water availability has been found in Mediterranean woody seedlings (Valladares *et al.,* 2002; Chambel *et al.,* 2004a). However, it has been found that not all coexisting plants exhibit the same levels of plasticity in a given stressful environment. In a comparative study of sympatric species, two evergreen oaks and two *Pistacia* species, Valladares *et al.* (2005b) have found significant differences in the extent and type of plasticity among these species. In fact, different populations of Mediterranean oaks exhibit different levels of phenotypic plasticity (Balaguer *et al.,* 2001; Gratani *et al.,* 2003). Fragmentation of Mediterranean forests and shrublands, may favour increased phenotypic plasticity over local adaptation (Sultan and Spencer, 2002). But whether this increased plasticity will enhance performance and survival of saplings in a global change scenario or make them more vulnerable to unpredictable environmental fluctuations remains uncertain.

Response facing interacting effects

Environmental factors operate simultaneously, leading to a complex set of interactive and indirect effects on plants. These interactions can complicate the understanding of the evolution of phenotypic plasticity in plants, since plastic responses to one factor (e.g. light) might be limited over evolutionary time due to negative implications with regards to other factors (e.g. water or temperature). For instance, while the interactions between drought and high light, have been widely investigated (Niinemets and Valladares, 2004), only a few studies provide quantitative knowledge of their real impact on the performance of Mediterranean plants (Valladares *et al.,* 2005a). Maximizing carbon gain in shaded environments requires shade acclimation, which in turn increases susceptibility to photo-inhibition (Niinemets *et al.,* 2003). Moreover, species specific shade tolerance can be significantly influenced by water availability, as observed in pine and oak seedlings (Sánchez-Gómez *et al.,* in press). Thus, there are clearly complex interactions between factors such as drought and shade involving physiological capabilities and plasticities as well as competitive factors.

Plant species of contrasting functional traits and plasticities co-occur in many ecosystems. High drought tolerance coupled with conservative water use and relatively high levels of plastic response to environment (a strategy observed for instance in *Quercus* sp. saplings) seems to render good results under current climatic conditions in Mediterranean environments (chronic drought alternated with seasonal rainfall), while the opposite syndrome (observed for instance in *Pistacia* saplings) could enhance performance under future scenarios characterized by extreme aridity and more erratic rainfalls. However, our understanding of the functional implications of phenotypic plasticity in multifactor environments (and all environments are multifactor to one extent or another) is limited. The real adaptive value of plasticity of woody plants in a global change scenario is contingent on the given combination of factors that operates in each habitat, and clearly deserves more attention due to its intrinsic complexity.

Genetic sources of phenotypic plasticity

Similarly to the evolutionary role of plasticity, the genetic mechanisms underlying phenotypic plasticity are object of intense scientific debate. Generally gathered under the term *Epigenetics,* this black box includes the multiplicity of gene regulatory sequences for the same trait (Smith, 1990), shifts in gene transcription and translation, DNA methylation (Pigliucci and Schmitt, 1999), pleiotropy (the effects on different traits by a single locus) and epistasis (interactions between different loci). In plants, the search for «genes for plasticity» is occupying a great deal of research activities in model species like *Arabidopsis* (Tian and Chen, 2001; Cervera *et al.,* 2002).

Why should we study phenotypic plasticity in forest trees?

Forest trees live in heterogeneous environmental conditions, both over a large generation time and at a geographical scale. In addition to the yearly changes in temperature, rainfall and photoperiod, environmental conditions change from seedlings to aged trees in light, water and nutrients availability. However, trees are not able to avoid adverse environmental conditions by moving (at least in one generation time). As a consequence, in order to survive and reproduce, long-lived forest trees must have very precise mechanisms to tune gene expression to environmental conditions.

The response of forest populations to environmental change is based on the amount of genetic variability to adapt to the new conditions by altering population structure, but also on the extent in which each individual is able to change its phenotype according to the environment, and the costs of this capability. As an example, Mediterranean pines live in quite contrasting ecological conditions, and the level of genetic diversity is poorly related to environmental heterogeneity (Chambel *et al.,* 2004b). Especially, *Pinus pinea* displays a quite low genetic diversity, but it can thrive in a wide range of climates and soils.

But, if plasticity plays a major role in the behaviour of forest populations, which are the mechanisms involved in gene expression through a long lifespan? Is there a tight relationship among the environmental heterogeneity (over time) and the amount of phenotypic plasticity? How does phenotypic plasticity evolve? To what extent has the environment shaped today's forests and how will they be able to face the challenges of the Global Change? These are exciting themes needing urgent answers that should be addressed using model tree species.

However, the use of forest species for the study of phenotypic plasticity poses some problems and challenges, many of them related to experimental design. Maternal effects are not easily removed in population or family experiments and paternal contribution differs between populations. For practical reasons, most experiments deal with juvenile traits, but their correlation with adult traits is often unknown. The main rationales for using seedlings is the critical importance of selection at early stages in forest trees (in *Pinus uncinata,* surviving seedling represent 0.7% of the seeds after the first summer) together with some promising results obtained with contrasted experimental protocols and early tests under controlled conditions. However, protocols are not widely accepted, underlining the need to choose some model species of rapid growth (i.e. poplars or eucalypts), or to combine molecular and phenotypic evaluation. On the other hand, reproductive fitness is difficult to assess and the most deeply studied traits, those of economic relevance (growth, survival, drought or frost resistance, etc.), are complex and its relationship to fitness is still obscure for most species.

Implications of Phenotypic plasticity in forest management

Besides the contribution of forest trees to elucidate the role of phenotypic plasticity, the particular way in which genotypes yield different phenotypes responding to the environment affects to almost every aspect in forest management and forest policies.

— As already stated, silviculture makes a wide use of phenotypic plasticity. Plastic responses are used, for example, to induce natural pruning by controlling density, as individuals under high density tend to produce branchless stems. Recruitment treatments use the phenotypic plasticity during the first stages of development as a main factor for seedling establishment. Even when many forest practices are still based in an old accumulated never-written lore, the knowledge of the different ability of a given species (or population) to deal with sharp changes in the forest micro-environment can be used to predict the result of new treatments.

— Breeding for improved forest reproductive materials implies the testing of candidate genotypes in a range of environments. Hence the higher or lower morphological plasticity (for example, yielding very good growth only in the best sites, but behaving poorly in unproductive sites), or a physiological plasticity conducive to a high morphological stability are central causes of concern.

— In the transfer or forest reproductive material, phenotypic plasticity (or its absence) should be used to define breeding zones and the areas in which a given material can be used with controlled or assumable risk.

— One of the main challenges in forest conservation genetics is the evaluation of adaptation and adaptability of different genetic resources to biotic or abiotic stresses. Phenotypic plasticity is of prime importance to define the ability of the target genotypes to respond to new conditions, and therefore to decide on the best conservation strategies to be applied.

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