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*Corresponding author

Shu Wang, College of Forestry, Forest Ecology Research Center, Guizhou University, Guiyang, 550025, China

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Opinion Article

The Strategies of Plants in Dealing with the Increase of Population Density

Shu Wang*

College of Forestry, Guizhou University, China

Opinion

The increase of population density, or the presence of intraspecific neighbors, is a common and important biotic factor, for plant species, in natural environments. It can result in variations in various resources as well as interactive relationships among individual plants [1]. Despite a substantial body of studies have been focused on this issue, it is still not well understood that how plants may respond to increased density via phenotypic plasticity. In one aspect, studies on the effects competition on plants often produce inconsistent even contradictory conclusions (see [2,3] for detail); in the other aspect, there have been rare studies on the effects of density on plans [4,5]. For example, except that the extra stem elongation has been considered as a typical response of "shade avoidance" [6], how plants modify the biomass allocated to other organs, such as leaves, roots, branches and reproductive modules, has been controversial. The lack of inconsistency in relevant studies is probably due to the variations in competition or density treatments, plant growth stage, and abiotic conditions in different studies [2,3]. As the phenotypic response at whole-plant level consists of many local responses at modular levels and their interactions [7], we also hope to know how a number of morphological traits may respond to the increase of density, and how the relationships among them (phenotypic integration) may vary in the processes of response. In the recent articles on this issue, with an annual species of Abutilon theophrasti Medicus (Malvaceae), we systematically investigated how plants respond to increased population density via biomass allocation [8], a number of morphological traits [2,3], plant architecture [9] and phenotypic integration, as well as the relationships between trait plasticity and canalization, and between trait plasticity and integration [10]. We found that:

1) In response to increased density, plants may first alter the pattern of biomass allocation, before producing allometric plasticity [8]. And the variation in allometric relationships among organs might be apparent plasticity, as these relationships also ca vary with growth stages. Nevertheless, the occurrence of apparent plasticity may signify intensified effects of density on plants.
2) The plastic response of plants to density may be complicated, since the increase of density had both facilitative and competitive effects, either above ground or below ground or both, the overall responses of plants depend on which effect is stronger than the other [2,3]. Therefore, sometimes no response in trait does not necessarily mean density has no effects, but rather that effects of competition and facilitation have been counteracted.
3) The trade-off phenomenon not only can occur between different organs or traits, but also can occur between modules at different positions [9]. In dealing with increased density, plants may enhance stem diameter, leaf size, petiole length and their mass in some layers (the units divided along the stem in the vertical direction by a certain distance), reduce them in other layers, for a better acquirement of sunlight while saving energy input.
4) As plant size can affect their influences on each other, growth stage and abiotic conditions often modify plant response to density via effects on plant size [2,3]. For example, when plants are small and below-ground resources are sufficient, individuals in a dense population may have facilitative effects on each other, which mainly occurs below ground; whereas when plants grow larger or below-ground resources are deficient, they may show canalized or decreased root allocation, as a result of intensified competition.
5) The plastic responses, though mostly passive ones, may lead to an increase of the level of integration (indicated by the increase of correlations among traits) [10]. However, decreased canalization due to increased density may facilitate active plastic responses in more favorable conditions or simply reflect adverse environmental effects. We emphasized that future studies should pay more attention to the abiotic and ontogenetic contexts of plant response to population density, and the complexity of such response when addressing this issue. It is also important to note that nature of phenotypic plasticity should not be simply the difference in final phenotypes, but rather that it suggests a capacity of plants to adapt to environmental changes, and this may cooperate with the ability of plants to maintain phenotypic stability.

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