

Benefits of the Carbon-Nutrient Balance Hypothesis

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The carbon-nutrient balance hypothesis (CNBH) is one of a number of approaches to understanding patterns of resource allocation in plants. Numerous empirical tests of the CNBH's predictions have led to certain key refinements and to the recognition that some of the simplifications inherent in the model limit its utility. However, as long as the model is applied to compounds with large pools, and the biosynthetic pathways of secondary metabolites are considered, the CNBH still serves as a useful guide for ecological research on resource allocation. One of the model's values is that it attempts to explain the plasticity of individuals but does not assume that all responses of individuals are optimal in terms of maximizing fitness.

The funeral oration for the carbon-nutrient balance hypothesis (CNBH) has recently appeared in the literature (Hamilton et al. 2001). As occurred with the first demise of Samuel Clemens, however, news of its death may have been somewhat exaggerated. For the 20 years since it was first explicitly stated in the pages of this journal, the CNBH inspired research and shaped our understanding of the behaviors of plants in response to variations in resource availability (Bryant et al. 1983). We argue that the CNBH still stands as a useful tool for exploring plasticity in plant defenses. Here we discuss some of the misconceptions surrounding the CNBH as well as some of the refinements that have emerged over the 20 years the hypothesis has been inspiring research.

Although the CNBH is one of many models examining the effects of resource availability on plant defense allocation, over the years it attracted much attention because of its focus on the scale of individual plasticity (Bryant et al. 1983). The CNBH suggests that when plants acquire resources in excess of growth demands, these resources are shunted into production of secondary metabolites. Thus, in situations with high light but limiting nutrients, plants are predicted to use the

“excess” carbon to produce carbon-based defenses such as phenolics. Similarly, if nutrients are abundant but light is limiting, plants are expected to increase production of nitrogen-based compounds such as alkaloids. One of the CNBH's strengths was its emphasis on the distinction between resources harvested below-ground (with roots) and those harvested above-ground (with leaves). This emphasis laid the groundwork for further more detailed efforts to combine physiological models of acquisition with whole-plant models of allocation.

One common criticism of the CNBH has been that it does not adequately predict defense differences among species or genotypes. This is an unfair criticism, as the CNBH specifically does not address *genetic* responses shaped by selection; it was designed to explain *plastic* responses of a particular genotype to variation in resource supply. We suggest that these criticisms of the CNBH arise due to confusion over the scales at which plants respond to resource availability. At one scale, there are genotypic responses where selection favors different levels of defense in different environments. Researchers working at this scale have developed a number of optimality models connecting resource availability to plant defense (e.g. Bloom et al. 1985, Coley et al. 1985). These models are appropriate for comparing defense allocation strategies across species, or across genotypes in different resource settings. On a different scale is the question of how a particular genotype or individual will respond to variation in resources. This response is the result of a plant's physiological ability to change allocation if the sizes of resource pools change. The CNBH specifically addresses this plastic response, and does not seek to explain the optimal defense levels around which this variation occurs.

In fact, one of the key insights of the CNBH is that it does *not* make claims for optimality, but simply argues that resources in excess of growth demands will be shunted into defenses. It is certainly possible that plasticity could be under selection and that regulatory enzymes would lead to adaptive responses. But it is equally possible that plastic responses are constrained by physiology and resource availability and are not always optimal. In fact, empirical studies support this *non*-optimal interpretation. For example, shade-adapted species invest more in carbon-based defenses such as tannins than do sun-adapted species, suggesting that it is better to have *more* defense in the shade. This agrees with predictions from optimality models such as the resource availability hypothesis (Coley et al. 1985). However, if one transplants an individual plant from the sun to the shade, tannin levels *decline* (Herms and Mattson 1992, Koricheva et al. 1998). This is consistent with the CNBH, and does not appear to be an adaptive response. Thus many examples exist where plastic responses do not mirror the optimal patterns seen across species. Further work would be necessary to demonstrate that these responses are not optimal, but it is intriguing that physiology may put constraints on the range of plastic responses that are possible, perhaps compromising plant performance under certain circumstances. The CNBH clearly points out this non-adaptive alternative, which should continue to be a valuable caution for interpreting one's results.

Another criticism of the CNBH has been that, as more empirical studies of the relationship between resource availability and allocation to defense have been conducted, the domain of the CNBH has grown more restricted. We view these restrictions as strengthening the hypothesis and as presenting new questions as to why the hypothesis works in some circumstances and not in others. For example, some of the most striking cross-taxon successes of any allocation model have come from applying the CNBH to products of the shikimic acid pathway, especially tannins. As predicted, studies on a huge range of plant species from many different biomes have consistently found an increase in tannins with increases in light or decreases in nutrients (Koricheva et al. 1998, Hamilton et al. 2001). Similar increases in phenols and tannins have been found for elevated CO₂ studies, which, like light-enhancement studies, increase the carbon/nutrient ratio within the plant (Lincoln et al. 1993, Lindroth 1996). However, results are much less conclusive for terpenes (products of the DOXP and mevalonic acid pathways) and alkaloids (a variety of pathways) (Koricheva et al. 1998). The apparent failure of these secondary metabolites to agree with predictions from the CNBH suggests that they might have different regulatory mechanisms than products of the shikimate pathway. Furthermore, even within

the shikimate pathway, condensed tannins and lignins respond to nitrogen fertilization as predicted by the CNBH, but hydrolyzable tannins do not (Haukioja et al. 1998, Koricheva et al. 1998). Haukioja and colleagues (Haukioja et al. 1998) suggest that this may be because condensed tannins and lignins are produced from phenylalanine and therefore compete directly with protein synthesis for nitrogen. A more complete understanding of the biosynthetic pathways would clarify where one would expect to find competition for resources and hence tradeoffs between investment in growth or defense, or between different classes of defenses. These differences in plasticity among secondary metabolites are intriguing and should inspire additional studies.

There is an honored (though contentious) tradition in ecological and evolutionary modeling of using data to refine and strengthen models (Parker and Maynard-Smith 1990). The last two decades have seen enough empirical work that these refinements can be put forth as generalizations that allow one to continue to use a modified version of the CNBH. Among the three most important of these refinements have been the following:

- 1) The recognition that, by its very structure, the CNBH is unlikely to be useful for understanding the regulation of compounds that are present in vanishingly small quantities. In one of the very first quantitative formalizations of the CNBH, Gulmon and Mooney (1986) point out that the cost-benefit approach is unlikely to be useful for compounds present in small amounts. In addition, there are significant technical constraints to measuring changes in compounds that are present at low concentrations. However, where defensive compounds make up a substantial fraction of leaf biomass or energy allocation, then the availability of resources may contribute to regulation (Reichardt et al. 1991).

- 2) The recognition that the major resource pools involved in production of a compound may lie in synthesis and/or storage, rather than in its skeleton (e.g. Mooney 1972, Margna 1977, Givnish 1986). Thus, to test the CNBH assertion that secondary metabolite production is influenced by substrate availability, we must understand enough of the biosynthetic pathways to account for all required resource pools. This may be particularly complicated for compounds such as alkaloids which include both nitrogen and carbon and are products of numerous interconnected biosynthetic pathways.

- 3) The recognition that secondary metabolites produced by pathways other than the shikimate pathway do not always (and may never) follow the predictions of the CNBH. This suggests that important differences exist in either the reliance on different resources or the regulation of different biosynthetic pathways. In addition, some secondary metabolites, such as al-

kaloids, are present in low concentrations and may be subject to the constraints outlined above (point 1).

Rather than discard the CNBH, we suggest using it as a first, but not final, step in studying the effects of resource availability on allocation to defense at the scale of individual plasticity. Perhaps the CNBH model will eventually be replaced by something more comprehensive that can explain a larger range of plant responses. Or, perhaps a better understanding of biosynthetic pathways and the resource pools involved in production of plant secondary metabolites will confirm the merit of the CNBH perspective. Nonetheless, we suggest that it is still worth considering the possibility raised by the CNBH that many plastic responses of plants to resource variation may be a consequence of substrate availability and not a result of regulated and adaptive responses. The importance of resources and the distinction between above- and below-ground resources in mediating allocation are also contributions of the CNBH and are likely to remain as guides in our investigations of plant ecology. Thus, we suggest that the successes and value of the CNBH should not be interred among the bones of its failures.

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