

- Mooney, H. A., and S. L. Gulmon. 1979. Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. Pp. 316-337 in O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (eds.), Topics in plant population biology. Columbia University Press, New York.
- Nobel, P. S., and P. W. Jordan. 1983. Transpiration analysis of desert species: resistances and capacitances for a  $C_3$ ,  $C_4$ , and a CAM plant. *Journal of Experimental Biology* 34:1379-1391.
- Orians, G. H., and O. T. Solbrig. 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *American Naturalist* 111:677-690.
- Raschke, K. 1979. Movements of stomata. Pp. 383-441 in W. Haupt and M. E. Feinleib (eds.), *Physiology of movements*, vol. 7, *Encyclopedia of plant physiology*, new series. Springer-Verlag, New York.
- Schaffer, W. M. 1977. Some observations on the evolution of reproductive rate and competitive ability in flowering plants. *Theoretical Population Biology* 11:90-104.
- Schaffer, W. M., R. S. Inouye, and T. S. Whittam. 1982. The dynamics of optimal energy allocation for an annual plant in a seasonal environment. *American Naturalist* 120:787-815.
- Schulze, E.-D., and A. E. Hall. 1982. Stomatal responses, water loss and  $CO_2$  assimilation rates of plants in contrasting environments. Pp. 181-230 in O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler (eds.), *Physiological plant ecology II*, vol. 12B, *Encyclopedia of plant physiology*, new series. Springer-Verlag, New York.
- Sugiyama, T., M. Miyuno, and M. Hayashi. 1984. Partitioning of nitrogen among ribulose-1,5-bisphosphate carboxylase/oxygenase, phosphoenolpyruvate carboxylase, and pyruvate orthophosphate dikinase as related to biomass productivity in maize seedlings. *Plant Physiology* 77:665-669.
- Tyree, M. T., M. A. Dixon, E. L. Tyree, and R. Johnson. 1984. Ultrasonic acoustic emission from the sapwood of cedar and hemlock: an examination of three hypotheses regarding cavitations. *Plant Physiology* 75:988-992.

# I The photosynthesis - nitrogen relationship in wild plants

CHRISTOPHER FIELD AND  
HAROLD A. MOONEY

Worldwide, nitrogen is one of the mineral nutrients most limiting to plant growth. Though it is the most abundant element in the atmosphere, nitrogen becomes available to plants largely through the recycling of organic matter or through the energetically expensive reduction of dinitrogen gas (see Chapter 10). Nitrogen is easily lost from ecosystems by leaching or conversion to  $N_2$  gas by denitrifying bacteria.

At the system level, the importance of nitrogen is underscored by the sensitivity of managed and natural ecosystems to nitrogen fertilization. Agricultural grain yield is highly correlated with the level of nitrogen application. This trend extends across a wide variety of crops and farming systems and includes the record yields of several crops (Ritchie 1980). Natural ecosystems respond to nitrogen fertilization with increased productivity or changes in species composition or both (Lee et al. 1983).

Nitrogen is a limiting resource in many ecosystems, but levels of leaf nitrogen reflect the relative partitioning among multiple sinks, as well as total availability. From an evolutionary perspective, the problem of nitrogen limitation has two components. How should a plant allocate a given nitrogen pool between reproduction, leaves, roots, and stems for the maximization of fitness? And, in any ecological setting, how big should the nitrogen pool be? Answering these questions requires knowledge of the costs of nitrogen acquisition and the benefits of alternative nitrogen deployment patterns. Mooney and Gulmon (1979, 1982) have established a conceptual framework for analyzing the costs and benefits of nitrogen acquisition and deployment, but the specific shapes of the cost and benefit functions remain somewhat conjectural. The relationship between photosynthesis and leaf nitrogen is one of the most important benefit functions, because photosynthesis provides the energy and structural substrates necessary for reproduction, growth, or foraging for additional nitrogen. Here we shall explore aspects of this benefit function, examining the generality, the mechanism, and some of the implications of the relationship between the photosynthesis and the nitrogen content of leaves.