DOES THE PLANT DEFEND ITSELF AGAINST LEAF-FEEDING INSECTS?

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Trees do not actively respond to herbivore grazing, they react to the deterioration in the balance of their roots and crowns functions, which comes when transpiration powers fall off. Such inherent reactions of plants originated as abilities to restore photosynthesis.

THE LARCH BUDMOTH SYSTEM

For example, every 9 years the larch budmoth, *Zeiraphera diniana* Gn., depletes the subalpine, larch-cembran pine forests (Baltensweiler and Fischlin 1988). The heaviest defoliations occur at altitudes of 1600-2100 m, last 2.93 $\pm$ 0.21 years, and recur at intervals of 8.47 $\pm$ 0.27 years. At lower altitudes defoliation occurs half as often and rather irregularly. Close scrutiny has shown that larch trees defoliated more than 50 percent refoliate in a manner similar to trees that have suffered from frost. In the spring following defoliation, needles are shorter than normal with increased raw fiber and decreased protein content. From 2 to 7 years after the outbreak, the needles recover their average quality, and the bud moth populations begin to grow along with the parasites which follow them. In the growth phase of the population cycle, the bud moth females lay 116 $\pm$ 19.1 eggs. Total generation mortality is approximately 90 percent and that gives rise to a 10-fold increase from one generation to the next. In the decline phase, the females lay 12.5 $\pm$ 19.1 eggs, larval parasitism increases 10-fold and the total mortality rises to 99.98 percent. Dendrochronological data observed in fossil larch dating from Roman times and in the beams of 15th century farm houses show that larch is adapted to defoliation and therefore the bud moth here is not a pest. The causes of bud moth density oscillations depend on weather, feeding, competition for food, predators, parasites, and pathogens.

THE GREEN OAK LEAFROLLER SYSTEM

The analysis of *Tortrix viridana* outbreaks in oak forests (Rafes 1989) is another example of this phenomenon. The devouring of foliage causes a hyperfunction of chloroplasts which restores the assimilation capacity to a small degree and only at the beginning of a serious grazing cycle. During hyperfunction and further formation of secondary leaves, the tree produces increased quantities of phenols and other antibiotics which accumulate in the leaves (Fagerstrom et al. 1987, Haukioja et al. 1985). The depletion of leaves diminishes the transpiration power of a crown and the water content of trees is reduced. During the period of crown depletion a great deal of the gnawed leaves, larval excrement, and entomophages fall to the floor; all of them stimulate the extraordinary activity of saprotrophs. A chemical analysis of soil at this time demonstrates an elevated content of nitrogen, phosphorous, and potassium. After the tortrix larvae pupate, the secondary foliage grows, but amounts to no more than 75 percent of the primary foliage. That is why the autumn leaf fall is only somewhat below the ordinary level. As a result of imperfect compensation, the growth in tree stem diameter

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drops off significantly. Throughout an outbreak, the enriching of soil with NPK favors to some degree the stand condition. But at the same time the accumulation of phenols and other antibiotics in foliage has adverse effects. They poison the tortrix larvae, its parasites, the soil, its inhabitants, and affect the roots of plants. Investigations in England (Carlisle et al. 1966) have demonstrated that an outbreak of *T. viridana* can bring about the serious change in the soil.

TAKING THE SYSTEM PERSPECTIVE

An insect outbreak is a symptom of forest ecosystem dysfunction. The quantitative relations of pests, their parasites, predators, and saprotrophs are disturbed, and their behavior becomes uncommon. Ecosystem function is suppressed as a whole and incapable of autoregulation. If it is sufficiently resilient it can be restored, but this is the matter of time. If it is not resilient, this ecosystem shall be changed.

At the introduction to the workshop "State and Change of Forest Ecosystems," Andersson (1984) considered trends of the problem: most attention has been devoted to the ecological importance of photosynthesis and the flow of organic matter in the food chains of biophages. But, nutrient formation and soil processes are understood imperfectly. In the monitoring of forest ecosystems, especially for the prognosis of pest outbreaks, chemical analysis of the dominant plant foliage and of the soils should be done for the physiological studies of phytophages and their host plants.

Ecosystem is the space-time unity in which all of motions are relative, i.e. interdependent. Mathematicians modeling ecosystems are forced to make a simplified schematic pattern of the interactions, but ecologist are obliged to reveal and to explain the causes of all phenomena occurring therein.

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