PHYTOTOXINS
NEW PROBLEMS IN FORESTRY?

PHYTOTOXINS have not received much attention from forest soil scientists or tree physiologists. The subject probably is unfamiliar to many practicing foresters. However, the basic idea that some trees or plants may produce substances which inhibit growth of other vegetation is not new. People working in agriculture and plant physiology have considered such possibilities for more than a century. In 1832 DeCandolle observed that certain species appeared to inhibit growth of associated species and suggested that toxic substances were involved (12). Shortly thereafter, the toxin theory became less popular and most adverse plant growth interactions were interpreted in terms of nutrient balances (6). Interest in toxic substances was not rekindled until the early 1900’s when organic toxins were isolated from a number of soils by USDA scientists (31, 33, 34). However, sufficient evidence to conclude that phytotoxins can play important roles in development of vegetation did not accumulate until the 1950’s and 1960’s.

Today there is little doubt that in certain situations organic substances produced by plants must be considered in managing agricultural and horticultural crops. How common or how important phytotoxic substances may be in timber production is in question, but recent work has suggested that we should not ignore this possibility. This paper reviews some aspects of the phytotoxin theory and cites some specific cases of phytotoxic effects of woody plants.

Nature of Phytotoxins

First of all, what are phytotoxins? They are plant-produced growth substances released to the environment which in small concentrations inhibit germination and growth of higher plants. Phytotoxins found to be ecologically important commonly fall into five chemical classes:

1. Phenolic acids have been isolated from a number of soils and plant tissues. Those believed to be associated with phytotoxic activity include p-hydroxy benzoic, gentisic, benzoic, salicylic, ferulic, and cinnamic acids.

2. Aldehydes—Salicylaldehyde was one of the toxins isolated in the early work at the Bureau of Soils and is one of the most toxic. Other toxic aldehydes are benzaldehyde and vanillin.

3. Coumarins include coumarin, esculetin, and scopoletin.

4. Glucosides include several of the phytotoxins of proven importance in woody plants. Juglone, the potent inhibitor of walnut, occurs as a glucoside in plant tissues which is readily hydrolyzed, then oxidized to juglone upon contact with air. Amygdalin and phlorizin, constituents of the bark of peach and apple roots, are glucosides which yield toxic products following transformation or decomposition by soil microbes. These toxins are involved in problems of replanting fruit orchards.

5. Terpenes—Recent work by Muller and his co-workers (9, 22, 24, 25) has indicated that terpene compounds such as camphor, cineole, and α-pinene may be involved in phytotoxic effects of certain woody plants in the Mediterranean climate of southern California.

How Phytotoxins Enter the Environment

All plants contain compounds which are capable of inhibiting growth if present in certain concentrations. However, release to the environment is a prerequisite for phytotoxic activity. Most workers believe that important phytotoxins are metabolic by-products or secondary metabolites and that plants must by some means prevent a build-up of such substances in their tissues (22, 26). The manner and rate at which the plant produces and releases such by-products will determine whether or not they are important ecologically. Phytotoxins are released through (1) decomposition of residues, and (2) excretion from various organs of living plants.

Decomposition of residues may release phytotoxins in certain cases (18, 27, 28). Many plants retain metabolic by-products in their tissues by a type of “local excretion” into vacuoles and cell walls (30). Toxic substances may be thereby rendered insoluble or nontoxic, or be incorporated into structural materials as is the case with lignin and flavonoid compounds.

Dean S. DeBell

JUNE 1970
These substances may be rendered toxic once again and released during microbial decay processes. Possible sources of phytotoxins resulting from microbial breakdown include forest litter, logging slash, and residual stumps and roots.

In other cases, accumulation of metabolic by-products is avoided by external excretion through roots (4, 5), leaves (36, 37), and possibly bark. When this occurs to any great extent, chemical interactions between living plants are possible. Mechanisms for release and removal of phytotoxins from living plants include crown leaching by rain or fog drip (9, 36, 37), volatilization from leaves (24), root exudation (4, 5), and branch and stem flow.

**How Environment Affects Phytotoxins**

Although many species produce and release substances with potential growth regulating properties, few seem to have phytotoxic effects on other plants. The substances often do not persist long enough to accumulate to toxic concentrations. Environment exerts great influence through effects on persistence and accumulation of toxins in the soil. In most cases where phytotoxins have been shown to be associated with decreased germination or growth, soils are characterized by heavy texture, poor aeration, excessive moisture, and often cool temperatures (17, 21, 32, 35). Under well-aerated and well-drained conditions, many phytotoxins resulting from both plant excretion and residue decomposition are rapidly metabolized by microorganisms into nontoxic forms (29). Where oxygen is limiting, organisms are lower in number and activity and such toxic substances persist. Soil colloids may be involved also in adsorption and retention of certain toxins (22). However, these are generalizations and certainly do not apply in all cases. Recent and current work by Muller (personal communication) has shown that different classes of phytotoxins persist optimally in different soil types.

**Mechanisms of Phytotoxin Action**

A wide range of injurious plant effects presumably are due to action of phytotoxins. This includes delay or complete inhibition of seed germination, general reduction in growth, root injury, and wilting. Until recently, little work had been done to determine the mechanisms through which toxic substances exerted these general effects.

Soil scientists may be interested in the possibility that phytotoxins affect mineral nutrition. Buchholtz (7) found that corn grown in association with quack grass suffered from severe nitrogen and potassium deficiency (even when fertilized). This was due to impaired ability to absorb nutrients when roots are in contact with quack grass infected soil. Reduced respiration and interference with ion absorption mechanisms, perhaps due to toxic substances, were suggested as possible causes.

Numerous cases are known where phytotoxins produced by a given species act selectively; that is, they affect one species more than another. The phytotoxins of *Salvia* (14), *Ailanthus* (20), and *Juglans* (19) have been demonstrated to affect certain species more than others. Although no literature is available on causes for selective action of phytotoxins, such selectivity could be due to differences in uptake, translocation, and chemical alteration of the substance in acceptor species. Such differences in response are known to be associated with the selective action of synthetic herbicides (1).

**Reports of Phytotoxic Effects of Woody Plants**

Let us now consider some examples of phytotoxic activity in woody plants. Perhaps the best known report is that of juglone produced by black walnut. Roots (8), bark (19), and leaves (3) probably contain the substance. Leaching of juglone from leaves by rain is thought to be the main cause of growth inhibition commonly found beneath walnut trees (3).

Concentrated work has also been done on phytotoxic substances associated with peach (27), guayule (5), *Encelia* (13, 38), and *Artemisia* (2, 11). Many other reports are based on field observations followed by little or no greenhouse and laboratory work, or on the inhibitory effects of plant extracts with no follow-up testing in the field. A condensation of such reports is available from the author.

In the last decade, considerable work has been done on a few species which appear to influence vegetation development in forests and rangelands. For example, Jameson (16, 17) found that growth of blue grama in Arizona rangelands was reduced in the presence of juniper trees. This inhibitory effect of juniper on heritage growth was most pronounced on heavy clay soils which were poorly drained and poorly aerated. Laboratory assays indicated that substances contained in juniper litter were involved. The active growth-inhibiting substances were found to include polymers and monomers of leucoanthocyanidins or catechins, plus another unidentified compound.

Muller and his students have done intensive work in the chaparral-grassland types of southern California (22, 23, 24). *Salvia* shrubs form small thickets dispersed throughout native, uncultivated grassland. Herbaceous vegetation is often absent beneath the shrubs and within a 6-foot radius of the shrub crowns. Though annuals become established beyond 6 feet, they are usually somewhat stunted; normal grassland development does not occur closer than 20 to 30 feet from these shrubs. Muller has shown that volatile terpenes are produced by *Salvia*. Inhibition of nearby grassland species presumably is due to these terpenes, especially camphor and cineole.

Vegetation development in *Eucalyptus* communities near Santa Barbara, Calif. has been studied by del Moral and Muller (9, 10). Volatile terpenes, fog drip from foliage, and litter leachates were involved in the absence of understory vegetation beneath canopies of *Eucalyptus globulus*. The same holds true for *E. camaldulensis*, except that fog drip is not a factor. Water soluble phenolic acids were isolated from fog drip and litter leachates. These included chlorogenic, *p*-coumaric, gentisic, ferulic, gallic, and caffeic acids. Inhibition beneath *Eucalyptus* was most extreme on heavy clay soils and absent on sands (del Moral, personal communication).
Such effects are not limited to arid regions of the West. A case of understory inhibition has also been reported in the humid southeast. Three years after a seed-tree cutting, Hook and Stubbs (15) noted that development of reproduction appeared to be retarded under oak seed trees, particularly cherrybark oak. Areas surrounding most seed trees of other species had experienced the tremendous burst of vegetative growth which normally accompanies harvest cuttings in fertile bottoms of coastal South Carolina. Hook and Stubbs suggested that root exudates or crown leachates might be causal factors. Subsequent work by the author which will be published elsewhere indicated that a phytotoxic substance leached from oak crowns was significant amounts of growth substances into the environment of major species is increasing and it seems likely that other species will be found which release significant amounts of growth substances into the environment. On certain sites, conditions may be such that these substances may persist and exert effects on other vegetation—possibly stimulatory as well as inhibitory. Effects and possible management uses of subtle factors of this nature should be evaluated if foresters intend to optimize productivity on forest lands.

**Conclusion**

Does this mean that foresters should consider phytotoxins in the management of forests and forest soils? Work on phytotoxins to date in most timber types is inadequate to answer this question decisively. However, emphasis on biochemical aspects of physiology and ecology of major species is increasing and it seems likely that other species will be found which release significant amounts of growth substances into the environment. On certain sites, conditions may be such that these substances may persist and exert effects on other vegetation—possibly stimulatory as well as inhibitory. Effects and possible management uses of subtle factors of this nature should be evaluated if foresters intend to optimize productivity on forest lands.

**Literature Cited**

22. **Scheiner**, S. 1977. Understory inhibition has also been noted that inhibition and redistribution of the leachate in plants. Amer. J. Bot. 54:116-121.