

CHEMICAL WELFARE IN THE FOREST

A Review of Allelopathy with regard to New Zealand Forestry.

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ABSTRACT

Allelopathy is reviewed and shown how it could relate to New Zealand forestry. The author speculates that allelopathy may be a significant factor in the following areas: the "replant problem", our understanding of competition between plants, and in the ecology of natural forests.

INTRODUCTION

"Allelopathy" is the term used to refer to certain biochemical interactions between all types of plants, including micro-organisms. The chemical exudates or leachates which are released from leaves, stems or roots (living or dead) can have an inhibitory or a stimulatory effect on other species or on the same species. The word does *not* refer to *direct* competition for water, minerals, food or light (Molisch, 1937).

"A rapidly growing body of data suggests that allelopathy is often important in the survival and growth of trees in both plantations and natural stands. An awareness of this phenomenon, and its potential effects on regeneration and site productivity, is essential in the practice of intensive silviculture". (Fisher, 1980).

"Phenomena previously attributed to competition for light, moisture, or minerals should be evaluated with a cognizance of possible allelopathic effects." (De Moral and Cates, 1971).

"The evidence is obviously accumulating rapidly indicating that many important forest tree species exert allelopathic effects against either herbaceous species or woody species or both. Such effects can no longer be ignored in forestry." (Rice, 1979).

Allelopathy has been known (though not under that name) for a long time. For example, Pliny the Elder reported the toxic relation of walnut to other plants (Plinius, first century B.C.). In addition, allelopathy is well known in folk lore. The non-specialist would usually consider, however, that allelopathy is a minor phenomenon restricted to exceptional species. Black walnut

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(*Juglans nigra*) is one of the best known (Massey, 1925; Schneiderhan, 1927; Brooks, 1951; Bode, 1958; Fisher, 1978; Funk *et al.*, 1979). Only since 1970 have research projects revealed the extent and potential importance of this subject (Rice, 1979). For example, Whittaker (1970) states that "allelopathy is not a peculiarity of a few plants but a widespread and normal, although mostly inconspicuous phenomenon of natural communities". Perhaps allelopathy could be detected in *any* plant, at least in the laboratory, given enough intensive research?

There is now a considerable literature on many aspects of allelopathy, but this article concentrates on those areas of research that appear to hold the greatest importance for forestry in New Zealand, although work in other areas (such as in agriculture) is relevant because it may serve to highlight the principles and processes by which this phenomenon operates.

As a caution it should be added that many of the experimental data are in need of verification, and many of the possible implications in this article are only speculation.

1. THE REPLANT OR REGENERATION PROBLEM

Numerous workers have found that second-rotation crops do not always grow as well as the first (for example Savory, 1966; Fisher 1980). For radiata pine, this has been noted in Australia (Keeves, 1966; Bednall, 1968) and even in New Zealand (Whyte, 1973), (although the latter is not very pronounced). The cause is tentatively attributed to nutrient deficiency, but this may not be the whole story or even the main factor. The allelopathic explanation for Whyte's observations will be discussed further under "general observations".

Chu-Chou (1978) has produced evidence that water extracts of root residues of radiata pine inhibit seedling growth of the same species. Pickett and Baskin (1973) suggest that the decay of roots may release allelopathics. Patrick (1955) reported the replant problem for peaches, Woods (1960) for jack pine, Florence and Crocker (1962) for *Eucalyptus pilularis*, Maliszewska and Moreau (1960) for *Abies alba*, Webb *et al.* (1967) for *Grevillea robusta*, and de Bell (1971) for cherrybark oak.

In horticulture this could be of some considerable economic importance as the replant problem has been observed for apples, grapes, cherries, plums, peaches, apricots and citrus and allelopathy is implicated in most of these (Proebsting and Gilmore, 1941; Patrick *et al.*, 1964).

Poor regeneration has often been noted in areas of our native forests, and many intriguing explanations have been offered. It is often said, for example, that the forest duff provides some sort of physical obstacle to seedling growth. This could well be true, but Molloy *et al.* (1978) found that aqueous extracts of fresh kahikatea leaves produced 100% mortality in kahikatea seedlings. Leaf extracts of matai and totara were also shown to be toxic. As will be discussed later, the ultimate effect of these toxins depends on many edaphic factors.

2. ESTABLISHMENT PROBLEMS DUE TO "COMPETITION"

Auto-inhibition as noted above appears to be less common, not surprisingly, than inhibition between species. Researched examples of the latter are too numerous to relate, but a few examples will suffice. Brown (1967) found that leaf extracts of nine species inhibited jackpine out of fifty-six species tested. Del Moral and Cates (1971) found allelopathic agents in nine of forty species investigated. Matveev (1977) found allelopathy in most of 47 species examined. Timofeev (1979) found that most of the above-ground plant parts of 12 species of ground flora inhibited germination and seedling development of Dahurian larch. Horsley (1977a,b) examined regeneration failure in black cherry and ruled out the effects of browsing, microclimate and competition for light and nutrients. He deduced that allelopathic inhibition by fern, grass, goldenrod and aster was the main cause.

(a) Grass "Competition"

Radiata pine planted directly into pasture does not succeed well (Tustin *et al.*, 1979). This is normally attributed to competition, for moisture. But Pickering (1903) concluded that the pernicious effects of grass on apple trees were due to a direct poisoning effect on apple roots, as did Howard (1925). Spurr and Barnes (1973) report that grass extracts inhibit hybrid poplar growth. Naturally, we must specify which species of grasses we are discussing. It cannot be assumed that all grass species share the same allelopathic properties.

Wheeler and Young (1979) found that fescue chemically inhibited loblolly pine. Rietveld (1975) discovered that *Festuca arizonica* reduced germination and early growth of ponderosa pine. Walters and Gilmore (1976) observed that *Festuca arundinacea* chemically inhibited sweetgum. Hilgendorf (1948) describes this species as being "excessively common on the heavy lands

from Wellington up both coasts at least as far north as the Waikato, and it is very difficult to eradicate".

Not all the research favours allelopathy. Webb and von Althen (1979) report that couch-grass affected sugar maple seedlings by competition and not by allelopathy.

The word "competition" is used very loosely in forestry circles. For example, the NZFS handbook (1982) on forest farming research at Tikitere declares (on p. 3) that "the trees and pasture compete for moisture, nutrients and light". Let the authors of this document substantiate their claim. They, and others, should carefully contemplate these words by Muller (1969):

"There is in the botanical literature a singular paucity of proven cases of plant competition in the field for water or for mineral nutrients. Few students of such competition have ever felt obliged to demonstrate that biochemical inhibition was not causally operative in the apparent cases of competition they were studying".

This sentiment is supported by Rice (1974) who says that: "virtually none of the papers I have read, which purported to demonstrate some aspect of competition, has in any way eliminated allelopathy as a possible cause of the observed results".

The exact cause of observed growth reductions is not an idle academic point. To facilitate an effective and efficient cure, we must make an accurate and precise diagnosis of the complaint.

(b) *Bracken "Competition"*

Torkildsen (1950) prepared an extract of bracken roots with cold, distilled water and found that it killed or dwarfed Norway spruce seedlings. Del Moral and Cates (1971) showed that bracken litter chemically inhibited Douglas fir. On the other hand, Stewart (1975) found that extracts of senescent bracken reduced germination in two species of *Rubus* but *not* in Douglas fir! Also Brown (1967) found that the *best* germination of jack pine occurred with bracken extract, from 56 plants tested. Giessman and Muller (1972) showed that the phytotoxin was leached from dead fronds, but not from living ones. They suggest that allelopathy is often the limiting factor on the growth of associated plants, rather than competition as is commonly supposed. Bohm and Tryon (1966) identified some toxins in bracken and in many other common ferns.

The same species of bracken (*Pteridium aquilinum*) occurs in New Zealand, albeit of a different variety. Even after good burns, bracken roots are still alive and could be exuding phytotoxins

harmful to young tree seedlings. If this is correct, then perhaps there is a case for herbicidal pretreatment of bracken, rather than mere burning, even if bracken regrowth does not cause competition as such.

(c) *Heather "Competition"*

Calluna vulgaris is a common exotic weed of the Central Volcanic Plateau (Healy 1973), and colonises a site very rapidly after a fire. Is this to the detriment of radiata seedlings planted in a heather matrix? For *Calluna vulgaris* is known to inhibit mycorrhizae of various tree species (Harley, 1952, Handley, 1963; Robinson, 1972; Mantilla *et al.*, 1975).

(d) *Hawkweed "Competition"*

Dawes and Maravolo (1973) found that hawkweed (*Hieracium aurantiacum* L.) inhibits tree seedlings. Makepeace (1976), working in New Zealand, found that *Hieracium pilosella* also produces phytotoxins. He says that *H. pilosella* is a drought-tolerant perennial that has become increasingly common in high country short tussock grassland in the past 25 years. *H. aurantiacum* is described by Hilgendorf (1948) as established in parts of Canterbury and making headway in tussock grassland near Cass.

(e) *Effects of Lichen*

New Zealand has many species of lichens that grow on bare ground, often beneath a manuka canopy. It is a rare forester that takes an interest in such small, seemingly insignificant plants. And yet Brown and Mikola (1974) and Fisher (1979) found that reindeer lichen has a very toxic effect on key mycorrhizae of jack pine. Leibundgut (1952) observed similar inhibition of *Pinus sylvestris*, *Pinus mugo* and *Picea abies*. New Zealand shares three species of lichen with those researched overseas: *Cladonia alpestris*, *Cetraria islandica* and *Cladonia pleurota*. These are known to cause inhibition, but the former two are not likely to be found in places where exotic planting would be undertaken (Martin and Child, 1972).

(f) *Sphagnum moss*

We do not plant radiata in places where sphagnum moss grows: the soil is too badly drained. We do, however, collect this plant and export it. This is a rapidly developing industry on the West Coast of the South Island, and the NZFS is involved as it controls much of the suitable land. Brown (1967) observed

that *Sphagnum capillaceum* contained phytotoxins. The significance of this becomes obvious when we consider that the main use of sphagnum is a plant growing or packing medium. The moss is of proven worth for general purposes, but perhaps certain species of commercial plant may be especially sensitive to any phytotoxins present.

3. PLANTING IN MIXTURES

We may be satisfied that radiata pine is best grown as a monoculture. For black walnut or Tasmanian blackwood, however, a mixture may be more suitable. But perhaps before we decide on a given combination, we should be aware of possible allelopathic interactions.

Funk *et al.* (1979) reported the deteterious effect of black walnut (*Juglans nigra*) on various coniferous seedlings: Japanese larch (*Larix leptolepis*), Norway spruce, eastern white pine (*Pinus strobus*) and Scots pine (*Pinus sylvestris*). The first and the last were killed by concentrations of juglone as low as 10^{-4} M. Perry (1932) observed that black walnut was capable of killing *Pinus strobus* and *Robinia pseudoacacia* growing in its vicinity. Given this, it is curious that the Forest Research Institute, Rotorua, report that "*Juglans nigra* grows well in association with *Robinia*, according to the American literature. The walnut responds well to the nitrogen supplied by the *Robinia*". (Errol Hay, 22 November 1979, pers. comm.). The answer probably lies in site differences, as is discussed later.

Leibundgut (1976) describes growth gains arising from judicious mixtures of trees. Often the gain can be attributed to the nitrogen fixation of one species (such as *Alnus incana* or *A. glutinosa*) providing benefit to a more valuable tree (such as *Picea abies*). But how does one explain the fact that larch (*Larix decidua*) increased Scots pine growth by 13% (remember that allelopathy is defined to include stimulation as well as inhibition).

Moreover, it might be unwise to rely on nitrogen fixation. Younger and Kapustka (1981) found that the nitrogen-fixing properties of *Alnus rugosa* experienced a 56.4% decrease due to the allelochemic effects of aspen (*Populus tremuloides*).

Kolesnichenko and Audryushchenko (1978) found that *Larix sibirica*, *Pinus sylvestris*, and *Betula verrucosa* chemically inhibited Norway spruce. Kolesnichenko and Kryukov (1978) found that ten well-known timber species inhibited *Quercus rubra*, and three provided stimulation. Leibundgut (1976) found that six

common timber species inhibited germination in *Pinus sylvestris*. Tubbs (1976) found that leachate of sugar maple (*Acer saccharum*) roots significantly retarded growth (after only 24 hours) of four out of five timber species. Kruger (1963) found that western red cedar produced substances toxic to Douglas fir. Chumakov and Aleikina (1977) showed that leachates of fallen leaves of five common trees inhibited various others.

Perusal of the above literature makes it obvious (if it is accepted that the experiments are valid) that allelopathy is not restricted to a few eccentric species, but is a common phenomenon of many if not most of our commercial species.

Obviously, the number of possible combinations of tree species is vast, and only a small number of combinations have been investigated. The logical procedure would be to list the mixtures that are in use or proposed for use in New Zealand (for example: Douglas fir/larch, *Eucalyptus regnans*/radiata pine, *Eucalyptus nitens*/*Acacia melanoxylon*) and to test these for allelopathy. If this is not done the danger is that, unless allelopathy is suspected, reduced growth in a crop species may be erroneously attributed to some other factor.

4. THE NATURAL DISTRIBUTION OF PLANTS

Much effort is devoted to the questions: Why does a tree grow on a certain site? What does this tell us about the tree? About the site? What are the underlying causes of the patterns and processes observed in natural ecosystems? A familiarity with allelopathy may be a prerequisite for this line of research.

For example, Tobiessen and Werner (1980) report that hardwood seedlings do not grow under *Pinus resinosa*, but they do under *Pinus sylvestris* in spite of the former having a higher light intensity and nitrate level. Allelopathy is implicated. Muller (1969) and Whittaker (1970) declare that allelopathy has been demonstrated to be capable of altering the structure, function and diversity of plant communities. Rietveld (1979) describes these general ecological implications of allelopathy.

The definition of a "tolerant" species requires greater precision. If a "tolerant" species is one that grows under a forest canopy, one could ask "but which canopy?" And if an "intolerant" species fails to grow under its own canopy, one could ask "is autoinhibition present?"

Pickett and Baskin (1973) suggest that allelopathy can function to change the rate of plant succession, to determine the compo-

sition of a seral stage, and even to halt succession by producing a "chemical climax".

5. TWO-TIER FARMING

Encouraged by the success of the Tikitere trials, one might assume that two-tier farming would succeed even better with a species that cast less shade than *Pinus radiata*. A deciduous species (for example a poplar hybrid) would allow grass to receive more winter sunlight. Eucalypts cast less shade because of the vertical habit of their leaves. But perhaps allelopathy should be considered first. We have dealt with the effect of grass on trees, and now we will consider the effect of trees on grass.

(a) *Eucalypts*

Del Moral and Muller (1969) noted that *Eucalyptus camaldulensis* inhibited improved grassland species including *Bromus mollis* and *Lolium multiflorum*. These (especially the latter) are of great importance in our pastures. They noted that there was 64% of full sunlight beneath the eucalypts but only 45% beneath *Quercus agrifolia*, and yet there was more vegetation under the latter. Interestingly, soil moisture in the litter zone was equal to or higher than in the open area, a phenomenon they attributed to the effect of shading and mulching. It is also interesting that Story (1967) quotes two experiments performed with *E. camaldulensis* and pasture species native to Australia. One worker found no reduction in pasture production under this species, while the other found improved production. How does one explain this discrepancy? One explanation would be that the native Australian grasses have developed an immunity to the phytotoxins present, whereas the grass species present in Iraq (*vide infra*) have not.

Al-Mousawi and Al-Naib (1975) observed a pronounced paucity of herbaceous plants in planted forests of *Eucalyptus microtheca* in central Iraq. Investigations revealed that the reduction was not primarily due to soil moisture, nutrient elements and shading. On the other hand, leaf extracts, decaying leaves and soil collected under *Eucalyptus* canopies inhibited seed germination and seedling growth of associated species. The volatile inhibitors were the same as identified for *E. globulus* by Del Moral and Muller (1969). These two researchers found that the absence of vegetation beneath *E. globulus* could not be attributed to competition for essential resources. On the other hand, phytotoxins in fog-drip (similar phytotoxins as for *E. camaldulensis*)

appeared to be capable of causing the observed effects. Grasses tested were *Bromus mollis*, *Lolium multiflorum*, *Bromus rigidus*, *Avena fatua*, *Festuca megalura*, and *Hordeum leporinum*. The first two were highly sensitive to the toxins and the last had greatest tolerance.

The variation in sensitivity of grass species could be of great importance for two-tier farming in a situation where allelopathy is an important factor in pasture suppression.

(b) *Poplars*

Evans (1981) suggests that poplars may (on fertile sites) be a better proposition for two-tier farming than radiata pine. But Del Moral and Cates (1971) found that *Populus trichocarpa* produced a volatile inhibitor, and Younger *et al.* (1980) found that freshly fallen leaf litter of *Populus tremuloides* had a phytotoxic effect on the grasses *Festuca elatior*, *F. rubra* and *Poa pratensis*. Curiously (in contrast to the previous section for eucalypts), and perhaps of economic significance, *Bromus inermis* and *Lolium perenne* were not affected.

(c) *Willows*

Brown (1967) noted that *Salix pellita* almost completely inhibited the germination of jack pine (*Pinus banksiana*). This may not tell us much about its relation to grass, but it does indicate that even the willow genus is not free from allelopathic activity. Kefeli and Turetskaya (1967) confirm this by observing allelopathy in *Salix rubra*.

(d) *Pines*

Lill and McWha (1976) found that vapour from decomposing *Pinus radiata* is inhibitory to white clover hypocotyl growth, to ryegrass (*Lolium perenne*) and, incidentally, to radiata seedlings. The toxic ingredient was ethylene. They doubted, however, that the effect would be detectable in the field. Chu-Chou (1978) discovered that *Pinus radiata* roots contained phytotoxins, but this does not mean that grass is necessarily affected. Jameson (1961) found that tree litter of Pinyon pine (*Pinus edulis*) was the major factor associated with reduction of blue grama grass (*Bouteloua gracilis*), and that tree cover as such did not influence blue grama or in some cases appeared to be beneficial. Lee and Monsi (1963) found that *Pinus densiflora* extracts markedly inhibited three species not usually found in pine forests.

(e) *Spruce*

Thomas (1974) found that aqueous extracts of blue spruce needles (*Picea pungens*) retarded or prevented seed germination or seedling growth of timothy, oats, wheat, barley and some lawn grasses. Titov (1971) describes continued studies on the growth of plots isolated from spruce roots by trenching and on untrenched plots. Results did not always support the idea that competition for water and nutrients is the main reason for elimination of grasses in spruce forests. Even when soil water and nutrients were maintained artificially at values optimum for the grasses, the spruce roots exerted an adverse effect on the grasses. Isolation from the spruce roots had a greater effect on the grasses than did fertiliser application.

(f) *Robinia*

Matveev *et al.* (1975) and Waks (1936) found that *Robinia pseudoacacia*, through allelopathy, caused a weak development of grass stands in the steppe zone of the USSR. This should cause people to pause who advocate a two-tier regime for *Robinia* for honey-production or for naturally-durable posts.

(g) *Black walnut*

The extremely high value of *Juglans nigra* is causing attention to be paid to the possibility of growing this on very fertile sites in New Zealand. Can we expect to graze profitably under these trees? I suggest that it probably depends on which species we choose for our pasture. Brooks (1951) recorded that juglone actually stimulated *Poa pratensis* growth.

(h) *Sycamore*

Al-Naib and Rice (1971) state that the failure of test species to grow under the canopy of *Platanus occidentalis* was not due to low minerals, water or light. On the other hand, decaying leaves, leaf leachate and soil collected under the sycamore canopy inhibited seed germination and seedling growth of many associated species. The latter included ryegrass (*Lolium multiflorum*) and *Poa pratensis*. Again, they noted that soil moisture was greater under the canopy at all sampling periods, than in the open.

(i) *Others*

Zolotukhin (1980) noted that Siberian pea-tree (*Caragana arborescens*) chemically inhibits couch-grass (*Agropyron repens*).

Jameson (1970) noted that the absence of blue grama grass under *Juniperus osteosperma* was due primarily to phytotoxins in the leaf litter. Buckenau (1883) and von Homeyer (1883) noted that grass in the early spring grew more luxuriantly beneath the spread of linden (*Tilia* sp.), beech (*Fagus* sp.) and maple (*Acer* sp.) than under poplar (*Populus* sp.), willow (*Salix* sp.) and birch (*Betula* sp.) due apparently to leachates from the various species. But were the leachates from the former stimulatory or were the leachates from the latter inhibitory?

Lodhi and Rice (1971) declare that "the failure of herbaceous species to grow well under hackberry (*Celtis laevigata*) was not due primarily to physical factors or to deficiencies in minerals, water or light". Del Moral and Muller (1969) suggest that the fog-drip from *Sequoia sempervirens*, *Pseudotsuga menziesii*, and *Cupressus macrocarpa* may be partially responsible for the striking paucity of herbs in forests dominated by these species. Oleksevich (1970) reported allelopathic activities in horse chestnut and fir. Podtelok (1972) found water extracts of roots of nine species of *Acer*, also *Quercus robur* and *Fraxinus excelsior*, were inhibitory. Corcoran (1970) reported allelopathy for carob (*Ceratonia siliqua*).

(j) Discussion

Note that with six species (*Eucalyptus camaldulensis*, *E. microtheca*, *E. globulus*, spruce, sycamore and hackberry) it was shown that competition occurring between trees and grass did not explain the reduction in grass growth. In fact the reduction could be explained wholly or largely in terms of allelopathy. It is therefore premature to explain reduction in pasture production under New Zealand two-tier regimes to the effect of competition. Competition may well be the correct explanation, but trials should be established to settle the point. Note that on page five of the Tikitere research publication previously quoted, one learns that "Ryegrass content of pastures is lower at higher tree densities; there has been no clear pattern of tree density on white clover". Why is this? Do radiata pine and white clover not compete, or is there a phytotoxin from the radiata which is selective to ryegrass?

Plants of the same species appear to vary considerably in their allelopathic potential (Putnam and Duke, 1974; Fay and Duke, 1977). Rice (1979) says "we are on the threshold of breeding crop plants that will inhibit the chief weeds in a given area through allelopathic action, and thus decrease the need for syn-

thetic weed killers. Imagine a self-releasing radiata seedling! Alternatively, we may be able to breed strains devoid of any allelopathic action, and thus achieve the maximum potential for two-tier farming.

The situation, however, is by no means simple. There is evidence, as we shall see, that competition and allelopathy interact in subtle and complicated ways.

6. GENERAL OBSERVATIONS

(a) *Nature of the Phytotoxins*

The study of allelopathy is by no means limited to observing the phenomenon in the laboratory and in the field. A large number of phytotoxins have been isolated, and for many of them their mode of action is known or suspected. The following list indicates the scope of the phenomenon.

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

2. *Aldehydes*. Salicylaldehyde was one of the first toxins isolated 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 oxidised 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*. 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 (de Bell, 1970).

(b) *Most Toxic Part of a Plant*

Del Moral and Cates (1971) analysed 40 plant species and concluded that chemicals leached from intact, living dicot leaves were, on the average, considerably more inhibitory than those

leached from either conifers or ferns. In nearly every individual case, litter extracts were substantially more inhibitory than leaf extracts of the same species. Matveev (1980) supports this finding.

(c) *Environmental Degradation*

Rice (1979) says that it is abundantly clear that if allelopathic compounds which are released into the environment were not decomposed, probably no plants could survive. Jameson (1970) says that "frequently inhibitors do not have any apparent ecological effect. If a small amount of material is deposited, or if the natural organic-matter breakdown processes proceed normally, little toxic material is accumulated. In some cases, however, material is deposited more rapidly than it is broken down, and species sensitive to these toxins are thereby influenced".

Rice (1979) continues: "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 . . . Under well-aerated and well-drained conditions may phytotoxins resulting from both plant excretion and residue decomposition are rapidly metabolised by micro-organisms into non-toxic forms".

This would certainly explain Whyte's findings that poor growth in some second rotation radiata pine forests occurred on the ridge tops and generally worse sites. (Whyte 1973). Whyte also found that ploughing the affected areas removed the problem, and in any case the effect disappeared given time (Whyte, 1982, pers. comm.).

If allelopathy is discovered to be a problem in two-tier farming, then this line of reasoning might act as a caution against restricting it to poor hill-country sites, rather than to the best soils.

Where drainage is poor the evidence is clear that phytotoxins accumulate. Del Moral and Muller (1970) say that "anaerobic conditions are not favourable to the metabolism of those micro-organisms responsible for the detoxification of phenolic compounds". Fisher (1978) confirms this by reporting that "on excessively drained sites, *Pinus resinosa* seemed unaffected by *Juglans nigra*, while on imperfectly drained sites walnuts suppressed or even killed the pines". In laboratory studies, he showed that juglone and its inhibitory activity readily disappeared under a "dry moisture regime" but remained under a "wet

moisture regime". Howard (1925) showed that aeration of the soil stopped fruit trees dying of "grass poisoning". De Bell (1970) says that "in most cases where phytotoxins have been shown to be associated with decreased germination or growth, soils are characterised by heavy texture, poor aeration, excessive moisture and often cool temperatures. However, these are generalisations and certainly do not apply in all cases. Recent work by Muller has shown that different classes of phytotoxins persist optimally in different soil types."

(d) *Synergistic Effects*

Watanabe *et al.* (1961) discovered a 20-fold increase in scopolin in leaves of tobacco plants that grew in a boron-free solution for 38 days. Dear and Aronoff (1965) found a pronounced increase in caffeic and chlorogenic acids in leaves and growing points of boron-deficient sunflower plants. This illustrates a certain point: it may be naive to attribute poor growth in the Nelson district, for example, to either boron deficiency or to allelopathy. The latter could be caused by the former. It is nonetheless important to pinpoint the precise mechanism involved: applications of boron may be ineffective if the damage has already been done by allowing the accumulation of toxins in the soil.

Del Moral (1972) discovered that increasing water-stress in sunflower plants increased total chlorogenic acid in the roots, stems and leaves. But the greatest increase in chlorogenic acid resulted from a combination of drought stress and nitrogen deficiency: this gave a 15-fold increase. This finding makes one suspect that competition and allelopathy cannot be considered in isolation.

SUMMARY

This review has tried to demonstrate that a knowledge of allelopathy may be essential to all who seek to study the growth of plants. Perhaps only a fraction of foresters have even heard the word "allelopathy". This is not necessarily because the subject is unimportant, but is because the bulk of the research has occurred only in the last decade, and the principles have not yet filtered down to the applied sciences. This paper is an attempt to introduce allelopathy to New Zealanders working with forestry, and to highlight the areas where this knowledge may make significant differences in our attitudes. In particular, changes in

our understanding of the "replant problem", competition between plants, and in the ecology of natural forests are postulated. It is suggested that allelopathy may be of vital significance in two-tier farming, especially if new species of tree or grass are considered. The actual implications of allelopathy can only be conjecture at this stage because New Zealand research in the field is as yet non-existent.

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